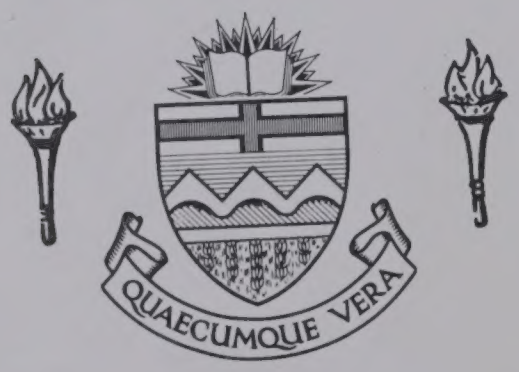
For Reference

NOT TO BE TAKEN FROM THIS ROOM

For Reference

NOT TO BE TAKEN FROM THIS ROOM

Ex libris
universitatis
albertaensis



The University of Alberta
Printing Department
Edmonton, Alberta

THE UNIVERSITY OF ALBERTA

RACIAL CHARACTERISTICS IN STOCKS OF ENGELMANNI RAINBOW

TROUT, Salmo gairdneri KIRTLANDI

BY

STUART HOWARD SMITH

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE

OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

MARCH, 1948

THE UNIVERSITY OF ALBERTA

RACIAL CHARACTERISTICS IN STOCKS OF ANADROMOUS RAINBOW TROUT, *Salmo gairdneri* RICHARDSON

by

STUART BOLAND SMITH

C

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

MARCH, 1968

STUART ROLAND SMITH

(C)

by

TROUT, Salmo dentiquest RICHARDSON

RACIAL CHARACTERISTICS IN STOCKS OF ANADROMOUS RAINBOW

THE UNIVERSITY OF ALBERTA

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE

OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

MARCH, 1988

UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled RACIAL CHARACTERISTICS IN STOCKS OF ANADROMOUS RAINBOW TROUT, SALMO GAIRDNERI RICHARDSON submitted by Stuart Boland Smith in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

Frontispiece. Summer steelhead leaping at obstacle in Coquihalla River, British Columbia, August, 1965. (For successful ascent, the leap is 11 feet vertical and 26 feet longitudinal.)

ABSTRACT

Wide differences were observed in state of sexual maturity in steelhead trout caught when entering spawning streams from salt water. Steelheads in a sexually immature state, entering streams largely between June and September were designated as "summer" fish and those entering in a sexually mature state, generally from November to May were designated as "winter" fish. Progeny from summer and winter fish from Capilano River, British Columbia were reared together, both in fresh and in salt water facilities, in order to determine the extent to which taxonomic and physiological characteristics are modified by the environment.

Taxonomic characteristics of experimental populations in general agree with the same characteristics in wild populations. These characteristics are heritable to the extent that meristic series, such as numbers of vertebrae, gill rakers and parr marks in F_1 yearling* fish can be used to separate summer and winter stocks. No character was found which could be used to separate individuals from the two stocks.

*The use of F_1 designation throughout this paper in all cases describes yearling or older first generation progeny from Capilano River parent stocks.

No intergrades were found between summer and winter fish with respect to physiological characteristics, such as rate of maturation in salt water and level of storage fat, both in juvenile and adult fish. Population samples from seven widely separated streams were compared with experimental populations. Maturation and fat storage characteristics in experimental populations provided evidence that different rates of sexual development, and sharply different migratory behaviour patterns, are strongly heritable.

Fecundity of summer steelheads is strongly affected by starvation during final maturation. Egg numbers are reduced in female summer steelheads, which resorb a large proportion of the number of eggs in the ovary during final maturation. Artificial fertilizations, including reciprocal crosses of summer and winter fish, indicated that summer and winter stocks are mutually viable. Number of mature eggs produced is a function of length of female, while differences in size of eggs from individual females are at least partially determined genetically.

Detailed examination of summer and winter F_1 progeny from Capilano River parent stocks suggests that the two varieties do not interbreed in that stream; samples from wild populations from six

other rivers provided data consistent with the same hypothesis. The available evidence suggests use of spawning habitat in streams in a manner that allows for reproductive isolation of summer and winter stocks. Reproductive isolation has probably occurred relatively recently, because of mutual viability of artificial crosses of summer and winter fish and because of relatively small differences in taxonomic characters.

ACKNOWLEDGEMENTS

The author is indebted to a large number of persons for aid and encouragement and for providing some of the data for this study. Dr. W. E. Ricker encouraged publication of a short note on summer and winter steelheads in 1960 and suggested that research in depth might be profitable. Dr. P. A. Larkin made many useful suggestions during the early phases of the work. Drs. C. C. Lindsey, T. G. Northcote and G. F. Hartman discussed various aspects of the problem with the author on a number of occasions. Their criticisms and some of their original ideas have been freely used.

During the time when fish were held in hatchery facilities of the British Columbia Fish and Wildlife Branch, many persons were involved in care and sampling of specimens. Mr. F. H. Martin, Supervisor at Cultus Lake and Abbotsford Trout Hatcheries, held and spawned Capilano River Steelheads and held steelheads from San Juan River until they matured. Mr. J. G. Terpenning sampled experimental groups of yearling steelheads and was responsible for supervision of all freshwater hatchery facilities throughout the study.

Mr. N. W. Green, Supervisor of Summerland Trout Hatchery, together with Mr. G. W. Paull, carried out spawning of F_1 Capilano River summer and winter steelheads. Mr. T. G. Halsey obtained samples of eggs from Kootenay Lake rainbow trout. Mr. Cliff Millenbach, Mr. John Johannson, Mr. Tom Inions and Mr. Marvin Hull, of the Washington State Department of Game provided steelhead eggs and adult specimens. Mr. Leo Van Tine provided specimens from Chilcotin River. Mr. C. E. Stenton assisted in obtaining summer steelheads from Capilano River. Mr. John Hall of the Greater Vancouver Water Board was responsible for operation of trapping facilities on Capilano River.

Examination of San Juan River was aided by Mr. Jack Lenfesty, Mr. Glen Jones, Mr. G. W. Taylor, Mr. Murray Galbraith and Mr. C. J. Bull. Drs. T. G. Northcote and G. F. Hartman assisted in electrofishing and seining on San Juan River and Dr. G. F. Hartman assisted in skin-diving observations of tagged steelheads.

When F_1 experimental steelheads were being held in saltwater facilities at the Pacific Biological Station of the Fisheries Research Board of Canada at Nanaimo, British Columbia, Dr. J. R. Brett made available hold-

ing facilities. Mr. Danny Pozar was responsible for care and maintenance of steelheads at Nanaimo.

Dr. Ferris Neave provided data and scale samples for high seas catches of steelheads in the Pacific Ocean and Mr. C. E. Atkinson made similar data available from records of the U. S. Fish and Wildlife Service. Mr. I. L. Withler made available unpublished data from which growth calculations were made on wild adult summer and winter steelheads from Capilano River.

The author is grateful for financial support from the University of Alberta, Edmonton, Alberta, the Institute of Fisheries at the University of British Columbia, Vancouver, British Columbia and the British Columbia Fish and Wildlife Branch of the British Columbia Department of Recreation and Conservation.

Dr. C. P. Hickman, Jr., was responsible for supervision of the study in the Department of Zoology, University of Alberta; his help and criticism was always valuable. Dr. D. M. Ross was Chairman of the committee responsible for this study to the Faculty of Graduate Studies, University of Alberta; his encouragement at several points in the study is gratefully acknowledged. At the University of Alberta also, Dr. G. E. Ball of the Department of Entomology provided

considerable help through refreshing discussions of the general problems involved in taxonomic investigations.

Mr. T. A. Drinkwater, Technical Division, Alberta Department of Lands and Forests, Edmonton, Alberta, kindly made available technical assistance during preparation of figures. Mr. W. West arranged for reproduction of the thesis. Mrs. Zena Paley typed the manuscript.

Finally, I am indebted to my wife Margaret Smith, for her encouragement and for her financial support, without which the successful prosecution of this work would not have been possible.

TABLE OF CONTENTS

TITLE PAGE i

ABSTRACT iv

ACKNOWLEDGEMENTS vii

TABLE OF CONTENTS. xi

LIST OF TABLES xiv

LIST OF FIGURES xvii

INTRODUCTION 1

MATERIAL AND METHODS 13

WILD STEELHEAD TROUT 13

EXPERIMENTAL STEELHEAD TROUT 18

ECOLOGICAL COMPARISONS. 22

RESULTS. 24

TAXONOMIC CHARACTERS IN NATURAL POPULATIONS 24

TAXONOMIC CHARACTERS IN EXPERIMENTAL POPULATIONS 26

Scale Row Counts 28

Vertebral Number 32

Gill Raker Structure 36

Gill Raker Numbers 37

Number of Parr-marks 42

Summary of Taxonomic Comparisons . . . 45

EGG SIZE IN STEELHEAD TROUT 46

Egg Size in Wild Steelheads. 46

Egg Size in Relation to Number of Vertebrae 47

Egg Size in Relation to Size of Females 52

Egg Size in Experimental Populations. 55

Summary of Egg Size Relationships. . . . 59

MATURATION CHARACTERISTICS IN EXPERIMENTAL FISH 60

Gonad Development in F_1 Steelheads in Fresh Water 62

Egg Production During Freshwater Maturation 67

Viability of Eggs From Steelheads Matured in Fresh Water 68

Summary of Maturation Experiments. . . . 72

Gonad Development in Salt Water. 73

MATURATION IN NATURE. 74

Atresia in Ovaries of Wild Steelheads 75

Gonad Development. 79

Weight Loss During Maturation. 81

BODY FAT IN STEELHEAD TROUT 88

Body Fat in Experimental Populations. 88

Body Fat in Wild Populations 91

Weight-length Relationships. 96

TEMPERATURE TOLERANCE IN YEARLING STEELHEADS 98

GROWTH CALCULATIONS 101

Scale/length Relationship. 101

Calculations of Fish Lengths From Scales. 102

Growth of Wild Summer and Winter Steelheads 105

MIGRATORY BEHAVIOUR 109

Summer Steelheads in San Juan River. 109

Winter Steelheads in San Juan River. 117

Summer Steelheads in Other Streams. 117

Winter Steelheads in Other Streams. 120

Summary of Migratory Behaviour 122

DISCUSSION 124

LITERATURE CITED 156

LIST OF TABLES

Table I Taxonomic data for adult summer and winter steelhead trout from eight Pacific coast streams 25

Table II Comparisons of scale counts, vertebral counts and upper and lower limb gill raker counts in adult summer and winter steelhead trout from eight Pacific coast streams 27

Table III Comparisons of oblique scale row counts in F_1 summer and winter steelhead trout 31

Table IV Comparisons of vertebral counts in F_1 summer and winter steelhead trout. . . 35

Table V Comparisons of gill raker numbers in F_1 summer and winter steelhead trout. . . 40

Table VI Comparisons of number of parr-marks in F_1 summer and winter steelhead trout 44

Table VII Correlation coefficients calculated for the relation of egg diameters and egg weights in Capilano River summer and winter steelhead trout 49

Table VIII Correlation coefficients calculated for the relation of female mean lengths and means of egg weights for six populations of steelhead trout and one population of non-anadromous rainbow trout. 54

Table IX Comparisons of F_2 egg weights from Capilano River summer and winter steelhead trout raised to maturity in fresh water 57

Table X Comparison of mortalities in egg lots from F_1 summer and winter steelhead trout, brought to maturity in fresh water 71

Table XI Follicular atresia in ovaries of steelhead trout from six British Columbia streams 76

Table XII Weight loss in female summer steelhead trout during maturation in San Juan River, British Columbia 83

Table XIII Change in body weight in wild, adult summer steelheads from San Juan River, British Columbia, held in a freshwater hatchery during final maturation of gonads 87

Table XIV Calculated lengths of wild summer and winter steelhead trout from Capilano River, British Columbia. (Numbers in brackets refer to sample size) 107

Table XV Events during migration of adult summer and winter steelhead trout from salt to fresh water and during final maturation and spawning in streams 153

LIST OF FIGURES

Fig. 1. Probable natural distribution of Salmo gairdneri in British Columbia and adjacent coastal waters, with probable natural North American distribution shown on inset 2

Fig. 2. Collection sites in British Columbia from which summer and winter steelheads were examined 14

Fig. 3. Distribution of some ocean catches of steelhead trout, 1955-1964. 16

Fig. 4. Number of oblique rows of scales, counted four scales above the lateral line, in F_1 summer and winter steelhead trout. 30

Fig. 5. Number of vertebrae in F_1 summer and winter steelhead trout. 34

Fig. 6. Number of gill rakers in F_1 summer and winter steelhead trout 39

Fig. 7. Number of parr-marks in F_1 summer and winter steelhead trout. 43

Fig. 8. Size of eggs in summer and winter steelheads from Capilano River, British Columbia, in summer steelheads

from Skamania, Washington, and in winter steelheads from Chambers Creek, Washington 48

Fig. 9. Relation between mean egg size and mean number of vertebrae in F_1 summer and winter steelhead trout. 51

Fig. 10. Relation between mean egg size and length of female in summer and winter steelhead trout raised to maturity in fresh water. 53

Fig. 11. Size of F_2 eggs obtained from summer and winter steelhead trout raised to maturity in fresh water. 58

Fig. 12. Relation between gonad weight and body weight in F_1 yearling summer steelhead trout. 64

Fig. 13. Relation between gonad weight and body weight in F_1 yearling winter steelhead trout. 65

Fig. 14. Relation between gonad weight and body weight in over-yearling F_1 summer and winter steelhead trout reared in fresh and in salt water, and in wild summer and winter steelhead trout captured from six British

Columbia streams 66

Fig. 15. Relation between length of female and number of eggs in summer and winter steelhead trout raised to maturity in fresh water. 69

Plate I. Gonad development in summer steelhead trout after leaving salt water. . . . 84

Fig. 16. Weight loss in summer steelhead trout during final maturation period in fresh water. 86

Plate II. Visceral fat on stomachs of yearling summer and winter steelhead trout 90

Fig. 17. Relation of visceral fat weight and body weight in F_1 yearling summer and winter steelhead trout. 92

Fig. 18. Relation between visceral fat weight and gonad weight in F_1 yearling summer and winter steelhead trout 93

Fig. 19. Relation between visceral fat weight and gonad weight in adult summer and winter steelhead trout at time of entry to spawning streams . . . 94

Fig. 20. Weight-length relationships in fresh and in salt water for F_1 summer and winter steelhead trout prior to maturation 99

Fig. 21. Weight-length relationships in adult summer and winter steelhead trout captured from British Columbia streams 100

Fig. 22. Relation between scale diameter and body length in steelhead trout. 103

Fig. 23. Method of calculating lengths from scales of steelhead trout 104

Fig. 24. San Juan River, British Columbia, showing tributaries and reference points related to migratory behaviour of summer steelhead trout . . . 110

Fig. 25. Water temperatures in San Juan River and Harris Creek during and following migration of summer steelheads from salt water into the river system in 1964 and 1965 116

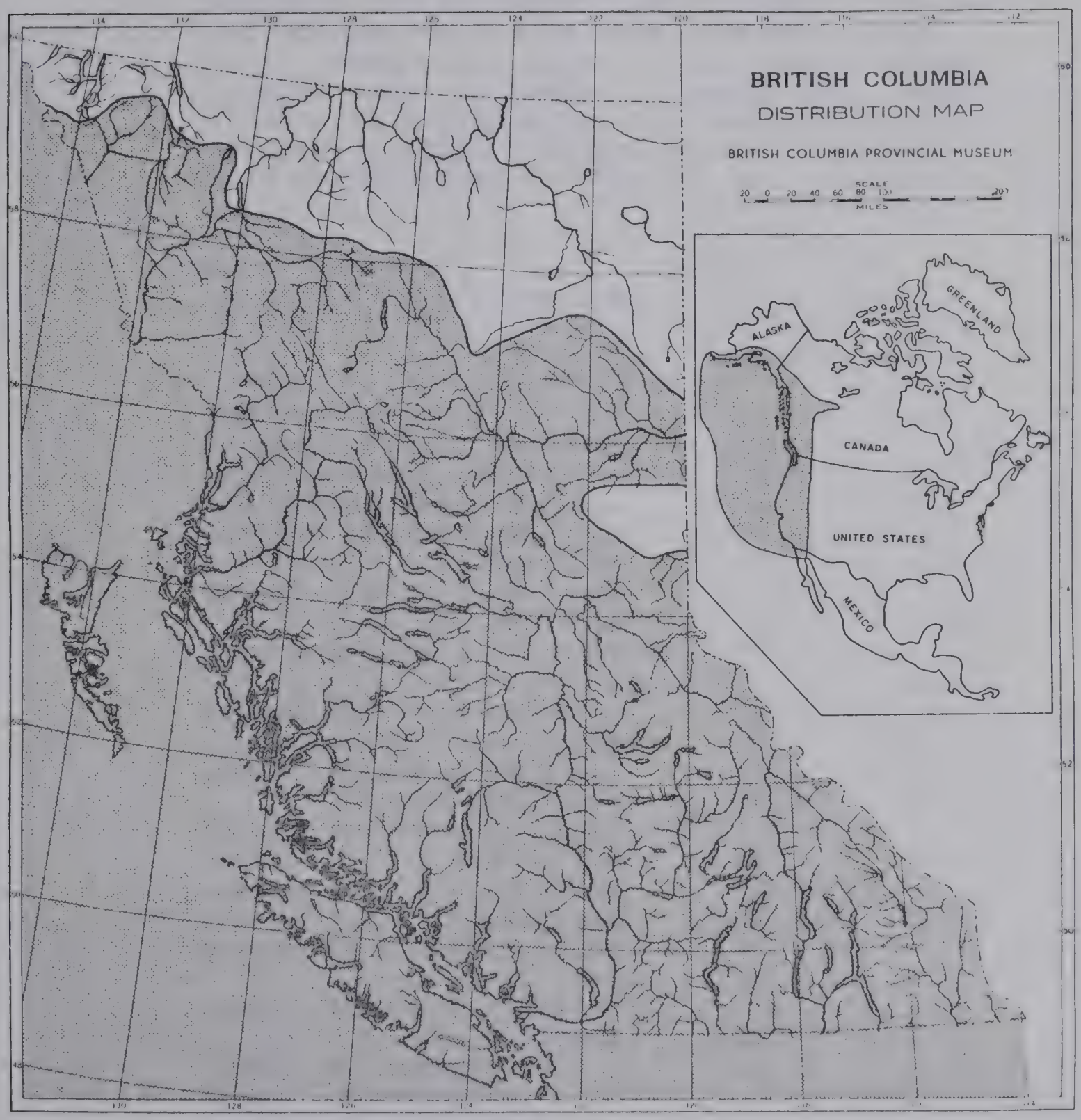
INTRODUCTION

Four well recognized species occur in the genus Salmo. In Europe and eastern North America, S. salar, (Atlantic salmon) is well known. The brown, or sea trout, S. trutta, originally occurred only in Europe, but has been introduced successfully both to the east and west coasts and to inland North America, to Chilean lakes and streams in South America and to New Zealand. S. gairdneri and S. clarki, the rainbow and cutthroat trout respectively, are both indigenous to western North America, but S. gairdneri has been introduced widely to many other regions and now occurs on all continental land masses as well as in Ceylon and New Zealand. S. gairdneri probably occurs also as an introduced species in many areas not recorded. Figure 1 shows the North American and British Columbia distribution of Salmo gairdneri.

Salmo gairdneri was first named by Sir John Richardson in 1836 from the Columbia River, and his description together with that of the collector is quoted below:

> "This species ascends the river in the month of June, in much smaller numbers than the quinnat, in whose company it is taken. Its average weight is between six and seven pounds.

Figure 1. Probable natural distribution of Salmo gairdneri in British Columbia and adjacent coastal waters, with probable natural North American distribution shown on inset.


BRITISH COLUMBIA
DISTRIBUTION MAP
BRITISH COLUMBIA PROVINCIAL MUSEUM
SCALE
20 0 20 40 60 80 100 200
MILES
ALASKA
GREENLAND
CANADA
UNITED STATES
MEXICO

Colour -- Back of head and body bluish-grey; sides ash-grey. Belly white. The only traces of variegated marking are a few faint spots at the root of the caudal. Form -- Profile of dorsal line nearly straight, tail terminating in a slightly semilunar outline. Ventrals correspond to commencement of dorsal and adipose to end of anal. Teeth -- Jaws fully armed with strong hooked teeth, except a small space in centre of upper jaw. Vomer armed with a double row for two-thirds of its anterior portion. Palate-bones also armed with strong teeth." Fins. -- Br. 11-12; V. 11; A. 12.

"DIMENSIONS

	Inches	Lines
Extreme length	31	0
Greatest height of body	5	9 1/2
Circumference of body	14	0
Breadth between the eyes	2	0
Breadth between the nostrils	1	2 1/3
Length from end of snout to nostrils	1	2 1/3
Length from end of snout to eyes	1	9 1/2
Length from end of snout to angle of opercule	5	2 1/3
Length from end of snout to pectorals	6	3 1/2
Length from end of snout to dorsal	12	0
Length from end of snout to ventrals	12	3 1/2
Length from end of snout to anal	21	0
Length from end of snout to *adipose	21	0
Length of pectorals	3	4 2/3
Length of ventrals	3	0
Length of attachment of dorsal	3	0

Height of dorsal	2	4 2/3
Height of adipose	1	2 1/3
Length of caudal	4	8 1/3
Its greatest breadth	4	0
Length of attachment of anal	2	4 2/3

Gairdner, in lit.

(In this species the gill-cover resembles that of S. salar still more strongly than that of the quinnat does, the shape of the subopercular in particular being precisely the same with that of salar. The teeth stand in bony sockets like those of the quinnat, but are scarcely so long. Those of the lower jaw and antermaxillaries are a little smaller than the lingual ones, and somewhat larger than the palatine or labial ones. The tongue contains six teeth on each side, the rows not parallel as in the quinnat, but diverging a little posteriorly. The pharyngeals are armed with small sharp teeth. The numbers of the teeth, excluding the small ones which fall off with the gums, are as follow: Intermax. 4-4; labials 21-21; lower jaw 11-11; palate bones 12-12; vomer lost; tongue 6-6. When the soft parts are entirely removed, the projecting under-edge of the articular piece of the lower jaw is acutely serrated, in which respect this species differs from all the others received from Dr. Gairdner. There are sixty-four vertebrae in the spine. -- R.)"

The description of "Gairdner's Salmon", as it was called by Richardson, is not incompatible with that which could describe summer-migrating anadromous rainbow trout.

Phenotypic variation in Salmonoidea probably is

greater in the rainbow trout complex than in any of the other related groups, including Salvelinus spp. (charrs), Coregonus and Prosopium spp. (whitefishes), Thymallus spp. (grayling) and Oncorhynchus spp. (Pacific salmons). As a consequence, early taxonomic work on rainbow trout described a large variety of forms, resulting in more than thirty nominal species, if the various forms of Salmo clarki (cutthroat trout) are included with the rainbows (Needham and Gard, 1959). More recently (Bailey, 1960), the rainbow trout has been consigned to a single species, although some biologists may recognize hereditary racial differences, particularly with respect to anadromy in Salmo (Rounsefell, 1958) or in genetic determination of some maturation characters in Salmo (Smith, 1960).

Commonly, the steelhead trout is recognized as that form of the rainbow trout which has spent some part of its life in the ocean, or if juvenile, as the progeny of oceangoing S. gairdneri. The steelhead is distributed widely on the Pacific coast of North America, from the California-Mexico border to Bristol Bay in Alaska (Carl et al, 1959). Typically,

steelheads spend the first two or three years of their lives in fresh water streams, although they also may migrate to the ocean at ages 0+, I+ and IV+. Typically also, mature or maturing adults return from the ocean to fresh water streams after two years in salt water, although in this case too, the life-history is somewhat variable and adults may return from the ocean one to four years after leaving fresh water. Adult migrant populations in a single stream may exhibit on their scales all the variations of stream or ocean residence noted above (Neave, 1949; Shapovalov and Taft, 1954; Maher and Larkin, 1955; Taylor and LeBrasseur, 1957; Withler, 1966).

The concept of so-called "seasonal races" of anadromous fishes was recognized more than thirty-five years ago (Rich and Holmes, 1929). Since then it has been widely accepted. Whether or not seasonal races are genetically distinct, or whether the characteristics of these stocks are largely controlled by environmental influences, is unknown for most populations. Recognizable races, runs or stocks (the terms often are used synonymously) may be separated by chronology of spawning migration, by differences in

rate of maturation, by differences in length of residence in fresh water or in the ocean, or by various combinations of these or other characters (Smith, 1960). Observations on the existence of races of salmonids are not confined solely to anadromous forms; Vernon (1957) demonstrated that significant, genetically controlled differences in morphological and other characters occurred in stocks of kokanee (non-anadromous sockeye salmon) in three areas of one large lake, even with about three percent straying between areas. Alm (1949) showed that some lake and river forms of Salmo trutta in Sweden differed in rate of maturation and in coloration of anal fins, and that differences persisted into the second and third generation, although the fish were reared under essentially the same environmental conditions.

Not all differences in migratory stocks of fish can be attributed to hereditary control. Lindsey et al (1959), in a study of inlet and outlet stream-spawning populations of rainbow trout in Loon Lake, British Columbia, observed that adults did not differ genetically in their responses to current, although 94% homing was observed for fish hatched in either of

the two streams studied. In that study, upstream migration of adults into the inlet stream could easily be the result of olfactory cues but downstream migration of adult spawning fish into the outlet stream could not be shown to be the result of known physical or chemical cues. Northcote (1962), in a study of the juvenile rainbow trout of Loon Lake showed that inlet and outlet stocks of these young fish did not maintain genetically discrete migratory behaviour patterns, but rather that water temperature was largely the controlling influence in migratory movement, both downstream in the inlet creek and upstream in the outlet. Ricker (1959) suggests that the number of stocks of Pacific salmon and steelhead trout in British Columbia alone is more than 10,000 and possibly as high as 50,000 depending on how distinct are the stocks of pink, chum and coho salmon in the numerous small streams where these fish have been observed to spawn. Ricker concludes:

> "..... that most of the studied differences between local stocks can and usually do have both a genetic and an environmental basis. Be it simple or

> complex, this should now be our normal expectation in respect to any as-yet-unstudied differences between stocks in Pacific salmonids."

Two seasonal stocks of steelhead trout are described in this paper: (1) "winter" fish, which enter fresh water from the ocean usually from December through March in a condition close to sexual maturity, and (2) "summer" fish, which usually enter streams between early May and early August, in a sexually immature state. Winter steelheads spawn in March through May, generally after they have been present in fresh water for no longer than 3 or 4 months, sometimes much less. Summer steelheads on the other hand, while spawning at much the same time as winter fish, usually have been present in fresh water from 7 to 10 months before spawning, and have spent a complete summer and winter in the spawning stream.

Typically, steelheads enter fresh water from the ocean with little external evidence of the secondary sexual characteristics usually associated with spawning rainbow trout. In males, development of teeth, hooking of the snout and red color on the

gill covers and along the lateral line may be totally absent, while females may retain the silvery appearance of ocean fish until spawning is well advanced.

In many British Columbia streams a noticeable "peak" occurs in upstream migration of steelhead trout. On the Thompson, Chilliwack (Vedder), Chehalis and Bella Coola Rivers, winter fish are present in the largest numbers from December through February. On Qualicum, Little Qualicum, Cheakamus and Nahatlatch Rivers, winter fish arrive from February through April, with the runs on the latter two rivers confined mainly to April and early May respectively. On other streams, such as the Coquihalla and Silver Rivers, near Hope, British Columbia, migration may be confined largely to summer fish, which enter these two streams mainly in May and June. On the Dean River and San Juan River, migration of summer steelheads is largely in July and August.

In at least two streams (Capilano and Seymour Rivers) both winter and summer steelheads may ascend from the ocean during the same period (April, May), although summer fish may continue to enter these two

rivers as late as mid-August in some years. So-called winter fish on Capilano River are heavy with sexual products and can easily be spawned shortly after they leave the ocean. On the other hand, summer fish migrating upstream at the same time as winter fish in Capilano River show almost complete absence of significant sexual development, and must be held from May or June until March or April in the year following until they can be spawned.

Such obvious differences as those cited for Capilano River summer and winter steelheads, migrating in the same river, in part during the same time of year, require careful investigation. Selective factors in the environment which favour differences in reproductive behaviour or in maturation rates can rapidly affect a plastic species, such as the rainbow trout. An important problem in the present case is therefore investigation of factors which permit (1) physiological differentiation, (2) reproductive isolation and (3) speciation. In this investigation, the a priori position is taken that stocks (races) of steelhead rainbow trout may exist as separate populations, even in the same stream, with little opportunity

for genetic interchange at the time of reproduction. The degree to which summer and winter steelhead approach the criteria of differentiation and isolation which permit speciation appears to be variable. To what extent these stocks exhibit characteristics which are genetically or environmentally controlled, is demonstrated by observations on wild fish and by comparisons of the two groups, reared experimentally under the same environmental conditions, both in fresh and in salt water.

A detailed examination of taxonomic and physiological characteristics of summer and winter steelheads is presented here in order to provide evidence both for differences and for similarities in these stocks of fish. Migratory ecology of summer and winter fish and certain life history data, are used to assess evolutionary tendencies in these stocks.

MATERIALS AND METHODS

WILD STEELHEAD TROUT

Within British Columbia, summer steelheads were obtained from San Juan River (23), Dean River (29), Capilano River (36); winter steelheads were examined from Capilano River (26), Chilcotin River (37), Qualicum River (11), Gold River (7). Outside British Columbia, winter steelheads were examined from Chambers Creek, in the State of Washington (22); summer steelheads were examined from the Columbia River at Skamania, Washington (17). On the first steelheads examined from Capilano River in 1958 (summer fish) and 1959 (winter fish) pyloric caeca were counted, but this character because of its wide variation was not recorded in subsequent samples from any stream. In the other samples listed above, fish were examined with respect to gill raker morphology and number, number of oblique scale rows four scales above the lateral line and for vertebral number. Vertebrae were counted in situ, after the flesh had been stripped from the right side of the fish. Gonad weight was determined to the nearest gram for all samples except those from Washington.

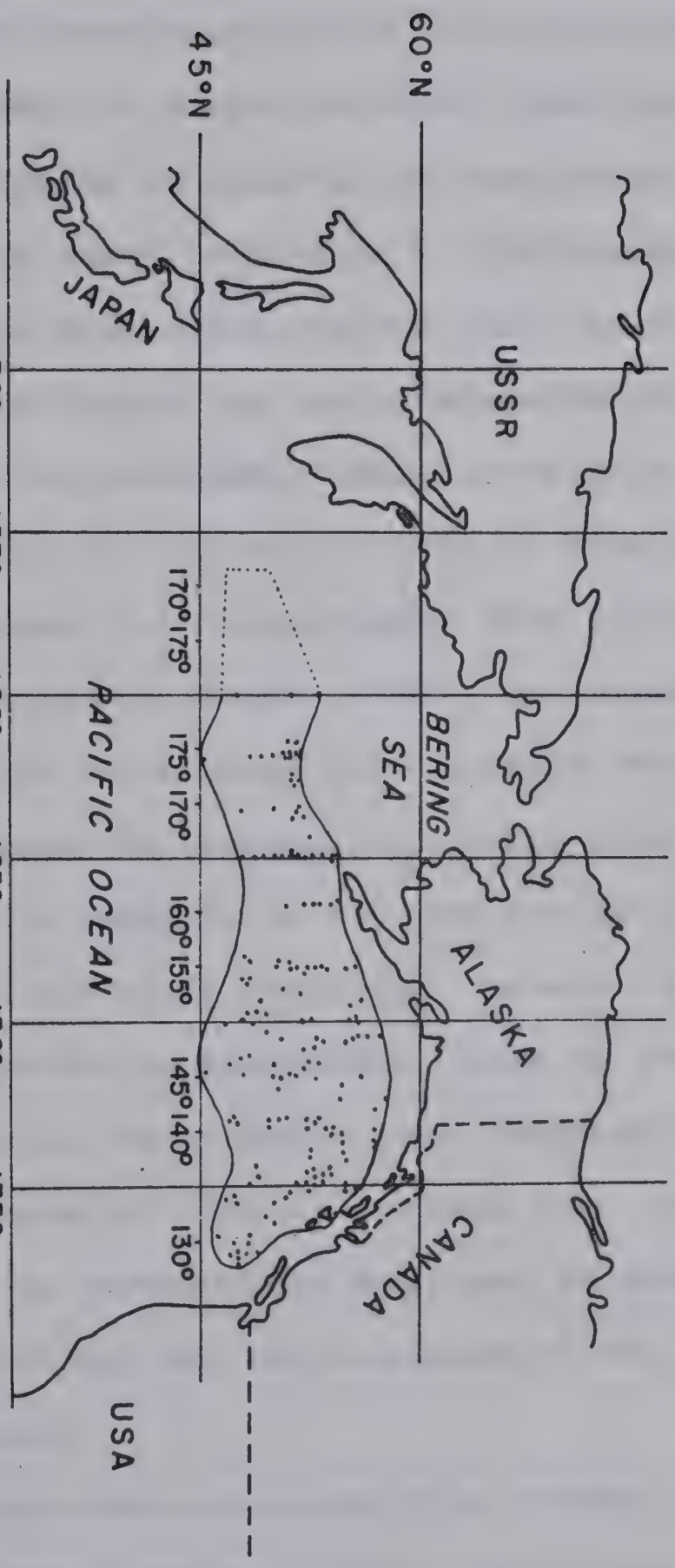
Figure 2. Collection sites in British Columbia from which summer and winter steelheads were examined.

BRITISH COLUMBIA
DISTRIBUTION MAP
BRITISH COLUMBIA PROVINCIAL MUSEUM
SCALE
20 0 20 40 60 80 100 200
MILES
STEELHEAD TROUT COLLECTIONS
IN BRITISH COLUMBIA
1 CAPILANO RIVER (26winter; 36summer)
2 SAN JUAN RIVER (23summer)
3 GOLD RIVER (7winter)
4 QUALICUM RIVER (11winter)
5 DEAN RIVER (29summer)
6 CHILCOTIN RIVER (37winter)
134
132
130
128
126
124
122
120
118
116
114
112
60
58
56
54
52
50
48

Figure 2 shows the areas in British Columbia from which adult wild steelhead trout were obtained, together with the number of specimens examined from each region. No attempt was made to collect summer and winter steelheads in all streams where both were known to occur, largely because of climatic conditions or stream flows, except for Capilano River, where permanent fish traps were operable at all seasons. Thus, in San Juan River and Dean River, only summer fish were obtained, although winter fish occur in both rivers. On Qualicum River and Chilcotin River summer steelheads have not been reported. It is known that summer steelheads pass through Gold River enroute to Heber River, an upstream tributary.

Fork length measurements and scale samples were obtained for Pacific Ocean specimens caught from 1955 through 1961 by vessels of the United States Fish and Wildlife Service, and of specimens caught from 1960 through 1963 by vessels of the Fisheries Research Board of Canada.

Figure 3. Distribution of some ocean catches of steelhead trout, 1955-1964. (The area enclosed by the dotted line has provided specimens to Japanese vessels, but steelheads from this region were not examined during this investigation.)


60°N
45°N
150°
165°
180°
165°
150°
135°
JAPAN
USSR
ARCTIC OCEAN
BERING SEA
ALASKA
CANADA
USA
PACIFIC OCEAN
170°
175°
175°
170°
160°
155°
145°
140°
130°

For the ocean-caught fish, it is not known to which of the summer or winter category they can be assigned. Distribution of catches of steelheads in the Pacific Ocean is shown in Figure 3. No taxonomic data were obtained from ocean-caught fish, which were used only for body length and scale measurements in subsequent growth calculations. Relationship of scale size to body size during marine life of steelhead trout was determined for ocean-caught fish in the same manner as outlined by Smith (1955); for steelheads in fresh water the scale-body relationship was determined separately for summer and winter steelheads from series of samples of the two stocks raised at Summerland Trout Hatchery. Growth of wild summer-run and winter-run steelheads, both in fresh water and in the marine environment, was compared by using calculated lengths of fish at various ages, as in Smith (1955), where the methodology employed in making growth calculations and the accuracy of the method is discussed in detail.

Eggs were obtained from summer and winter steelheads from Capilano River; from winter steelheads from Chambers Creek, near Tacoma, Washington; from summer

steelheads spawned at Skamania Hatchery (Columbia River), State of Washington. Sizes of eggs from each adult female steelhead were compared by weighing individual eggs to the nearest mgm on a Roller-Smith balance, rather than by measuring egg diameter. Relationship of egg weight to egg diameter was determined for nine fish.

EXPERIMENTAL STEELHEAD TROUT

Wild summer steelheads were trapped from Capilano River in August 1959 and transported to Cultus Lake Trout Hatchery, where they were held until they matured in April 1960. Winter steelheads were trapped in April, 1960 from Capilano River and also were transported to Cultus Lake Trout Hatchery. Both summer and winter females were taken from the retention ponds and killed by cutting the ventral aorta posterior to the isthmus. All females were placed in racks in the head down position until bleeding ceased. Females were then incised and all eggs removed to dry pans. Each lot of eggs from individual females were fertilized with sperms from individual males. Eleven lots of eggs from summer fish and seven lots of eggs from winter fish were

each held in separate compartments and hatched separately in order that parent history could be known for all groups of progeny. From the eggs obtained from Capilano River winter and summer steelhead in 1960, fry and fingerlings were retained at Cultus Lake Trout Hatchery for experimental purposes.

In May, 1961, a total of 549 yearling steelheads were sacrificed and preserved for later examination. A minimum of 30 yearlings were preserved from each of the 18 groups. Environmental conditions were uniform for all 18 groups from the time of egg fertilization throughout all subsequent experimental rearing procedures. Initially, each group lot was branded with a number, by using a heated branding iron and in addition, winter steelheads were marked by removal of the adipose fin. All remaining fish were then confined in a single rearing pond. Examination of the fish in all groups six months after branding revealed that the brands could not then be identified, thus individual parental history was no longer traceable in these F_1 progeny.

From the 549 yearling fish samples taken in 1961, comparisons were made between winter and summer stocks and between groups of young fish from individual female parents within each stock. For meristic comparisons counts were made of vertebrae, scale rows, parr marks, gill rakers; for physiological comparisons body weights and weights of visceral fat and gonads were determined.

Approximately 300 F_1 progeny from the 11 summer and 300 from the 7 winter groups were transferred to Summerland Hatchery as yearlings in 1961 and reared to maturity at that location. Samples of F_2 eggs from mature females in these groups were obtained from each of 30 females in the two stocks. Egg number and size and mortality rates of fertilized eggs were determined for fertilizations of summer X summer, winter X winter, and reciprocal crosses. Egg number was also determined for all remaining unspawned females of each stock (90 winter-run fish and 75 summer-run fish).

From the original fertilization of Capilano River steelheads, approximately 200 yearling summer and 200 yearling winter steelheads were transferred

to salt water facilities at the Pacific Biological Station, Nanaimo, British Columbia, and reared for three years at that location. Maturation rates were determined by weighing gonads and weights were taken also of visceral fat for these F_1 fish in both stocks. Scale samples were obtained for subsequent determination of the scale/body-length relationship in salt water for various sizes of fish.

During the period July 18 - 31, 1961 lethal temperature comparisons were made on the Capilano River F_1 summer and winter steelhead trout at the Fish and Game Branch trout hatchery at Summerland, British Columbia. Equipment used (temperature regulators, tanks, etc.) was the same as that described by Black (1952). It was known from Black's work that the upper lethal temperature for non-anadromous Salmo gairdneri (Kamloops trout) was slightly over 25° C for fish acclimated at 11° C at Summerland hatchery. Accordingly, all fish in the two strains were exposed to a temperature of 25 $\pm$ 0.2° C in groups of ten fish in each test. Resistance time was determined by recording the time to death of the fifth specimen (LD50). Death was

presumed when opercular movements could no longer be observed. Preliminary tests with steelheads had indicated that death of 50% of the fish would occur at a time exceeding two hours duration. During the first few tests, deaths of all specimens were recorded, but in most of the latter tests, no observation was made before two hours' exposure had elapsed. Tests were replicated twenty-two times, involving 220 fish in each strain.

ECOLOGICAL COMPARISONS

During 1963 through 1965, field examinations were made of the San Juan river system, on southern Vancouver Island. Temperature records on the two main stems of this river system (Harris Creek, San Juan River) were obtained in 1964 and 1965. During the summer of 1964 (July, August), summer steelheads in San Juan River were tagged with Peterson disc tags. Recoveries of tags from angler-caught steelheads, together with sightings of tagged fish by skin divers, were used to assess distribution and migratory behaviour of summer fish in the San Juan river system. Flows on the San Juan River and its tributaries are generally very high during winter months (November to

March); the investigation of migratory behaviour of winter steelheads is not possible without the installation of fish fences and traps, and therefore was not assessed on this river system.

RESULTS

TAXONOMIC CHARACTERS IN NATURAL POPULATIONS

Examination of young summer and winter steelheads from Capilano stocks had indicated a wide variability in all characteristics except vertebral, gill raker and parr mark number and amount of visceral fat. Taxonomic characters in samples of adult fish from the several rivers listed above were compared with respect to four meristic series. These data are listed in Table I. Comparisons of the meristic series in samples from different streams revealed no statistically significant differences in population samples within each stock; all winter steelhead samples were therefore combined and compared with the total summer steelhead samples. Table II lists the frequencies of vertebra, scale and gill raker number in each stock, together with statistical values calculated for comparison of the appropriate meristic series. It is apparent from these comparisons that except for scale rows, wild summer and winter steelheads can be statistically assigned to separate populations with a considerable degree of certainty, although

Table I Taxonomic data for adult summer and winter steelhead trout from eight Pacific coast streams.

	Source of fish	Number of specimens	Mean number of vertebrae	Mean number of gill rakers			Mean number of oblique scale rows
				upper limb	lower limb	total	
Summer steelhead	Capilano River	36	62.03 (60-63)	7.82 (7-9)	10.75 (9-12)	18.59 (17-21)	141.92 (130-154)
	San Juan River	23	61.48 (60-63)	7.96 (7-9)	10.61 (10-13)	18.56 (17-21)	132.30 (122-156)
	Dean River	29	61.89 (60.63)	7.72 (7-9)	11.68 (10-13)	19.38 (17-21)	130.24 (129-149)
	Columbia River	30	62.11 (61-63)	7.76 (7-9)	10.93 (9-13)	18.71 (17-21)	135.43 (126-151
Winter steelhead	Capilano River	26	63.13 (62-64)	7.73 (7-8)	11.43 (10-13)	19.21 (17-21)	138.43 (121-160)
	Chilcotin River	37	63.10 (61-63)	7.56 (7-9)	11.52 (10-13)	19.09 (17-21)	140.71 (124-162)
	Qualicum River	11	62.80 (62-64)	7.54 (7-8)	11.09 (10-12)	18.56 (17-20)	138.97 (122-160)
	Gold River	7	63.00 (62-64)	7.71 (7-8)	11.00 (10-12)	18.64 (17-20)	132.66 (129-140)
	Chambers Creek	22	62.95 (61-63)	7.59 (7-9)	11.41 (10-13)	18.09 (17-21)	136.24 (126-162)

Ranges in number of vertebrae, gill rakers and oblique rows of scales are shown in brackets below each mean value.

ranges in characters overlapped in all samples.

Because the ranges in gill raker, scale row and vertebral number overlap almost completely, single specimens cannot be assigned to one stock or another. Further, nothing is known of temperature or other environmental conditions during the period of egg incubation of these stocks. Thus the meristic differences described above could be controlled in part at least, by environmental conditions during somite formation. It is clear however, that meristic series are consistent for all samples, and in view of evidence to be presented in the following section, it is suggested that meristic differences are at least partly heritable.

TAXONOMIC CHARACTERS IN EXPERIMENTAL POPULATIONS

External characteristics of young steelhead trout are so similar that they offer little opportunity for obvious separation of summer and winter stocks. Nevertheless, where large differences in physiological characteristics exist in adult fish (Smith, 1960) careful examination of taxonomic characteristics in their progeny is warranted. Meristic comparisons were made of scale, gill raker,

Table II Comparisons* of scale counts, vertebral counts and upper and lower limb gill raker counts in adult summer and winter steelhead trout from eight Pacific coast streams.

	Number in series	Summer steelhead	Winter steelhead	Totals	Value of X^2
Number of vertebrae	61 or less	30	2	32	
	62	39	22	61	64.9**
	63 or more	17	61	78	
Number of upper limb gill rakers	7	17	42	59	27.6**
	8	57	59	116	
	9	15	3	18	
Number of lower limb gill rakers	10 or less	19	9	28	25.2**
	11	49	55	104	
	12 or more	21	40	61	
Number of lateral line scales	<130-134	14	32	46	
	135-139	20	23	43	3.87
	140-144	21	25	46	
	145-149	26	6	32	
	150 or more	8	15	23	

*Sample sizes are not the same as in Table I (p. 25) (In certain cases, samples were of fish caught by anglers, who submitted only the head or defleshed carcass.)

**Probability less than 0.01

parr-mark and vertebral counts. Because all fish used in the following comparisons were hatched and reared under the same environmental conditions, statistically significant differences in any characters between stocks must be genotypic. Differences in soft part anatomy of these ;fish are described elsewhere, and it is an arbitrary choice whether to assign soft tissues to physiological or taxonomic categories.

Scale Row Counts

In many salmonids, the number of oblique scale rows intersecting the lateral line may be useful in separation of genera and species, but in rainbow trout this character is subject to wide variation. For 11 F_1 yearling groups of summer and 6 F_1 yearling groups of winter steelheads from Capilano River parents, scale row counts were made on 510 specimens. Each group of F_1 yearlings consisted of 30 fish from a single female, whose eggs were fertilized by sperm from a single male. These same groups of F_1 yearlings were also used for subsequent comparisons of vertebral, gill raker and parr-mark numbers. Oblique rows of scales were

counted four scales above the lateral line, under magnification varying from 2X to 10X, depending on the size of the specimen. Total range in scale count for winter fish was 120 to 160 and for summer fish was 123 to 158, except for one aberrant group of winter fish of which only 20 out of 300 survived to yearling age. This group of fish was also aberrant in vertebral counts compared to all others examined and occurrence of deformities was high. These fish were not included in this or subsequent statistical comparisons. Frequency distributions of scale counts for the two stocks is shown in Figure 4. It is apparent from Figure 4 that scale counts tend to be very nearly the same in summer and winter fish, and any difference is not significant ($P > 0.05$). The statistical comparison is presented in Table III.

Figure 4. Number of oblique rows of scales, counted four scales above the lateral line in F_1 summer and winter steelhead trout from Capilano River, British Columbia.

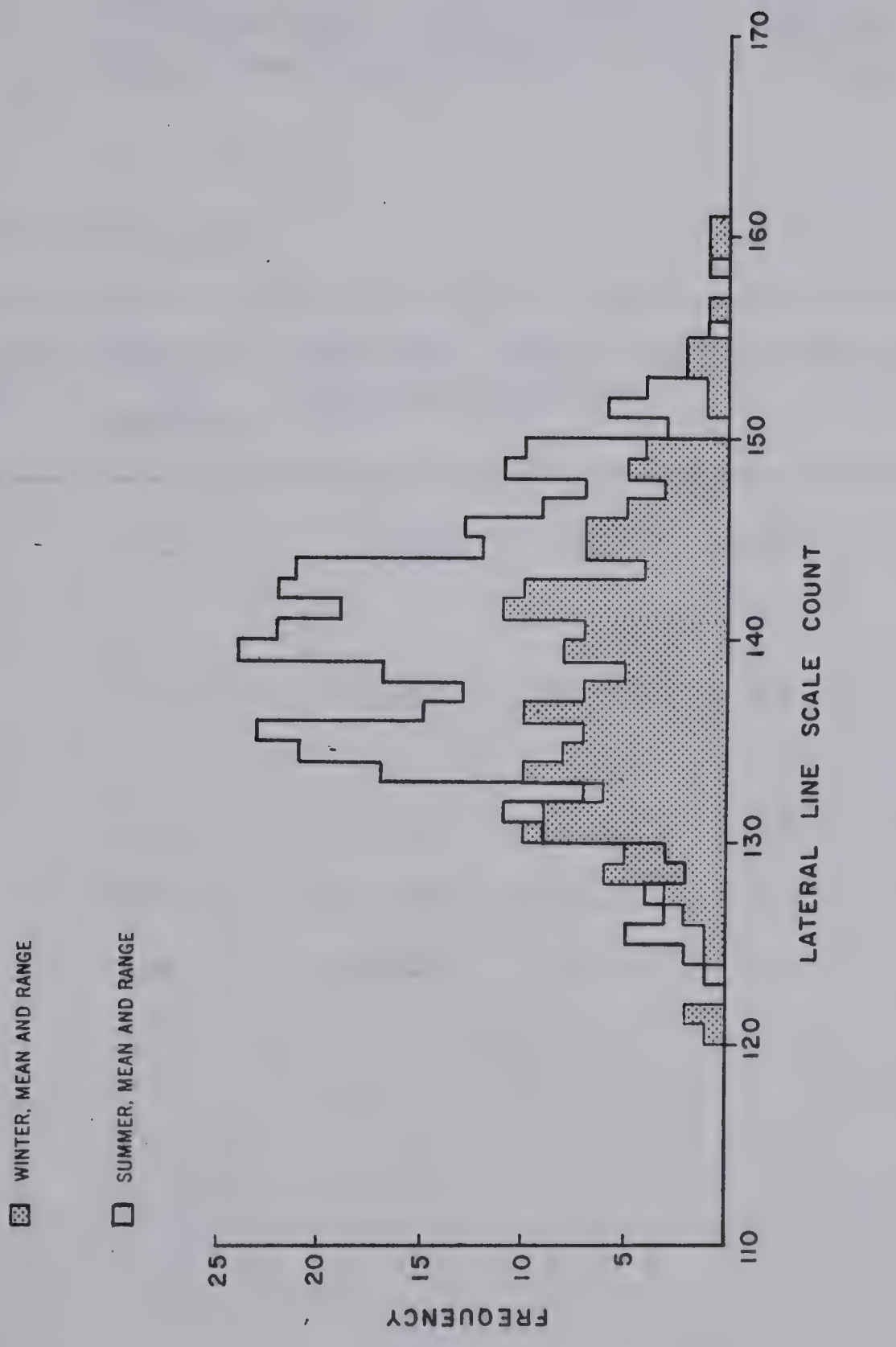

WINTER, MEAN AND RANGE
SUMMER, MEAN AND RANGE
FREQUENCY
25
20
15
10
5
110
120
130
140
150
160
170
LATERAL LINE SCALE COUNT

Table III Comparison of oblique scale row counts in F_1 summer and winter yearling steelhead trout from Capilano River, British Columbia.

Analysis of Variance

Sources of Variation	Degrees of Freedom	Sums of Squares	Mean Squares	Calculated F	1% Table F
Between Stocks	1	218	218	0.38	6.63
Within Summer Stock	10	3,624	362.4	0.64	2.32
Within Winter Stock	5	2,705	541.0	0.95	3.02
Error	492	27,876	566.0	-	-
Total	509	34,423	-	-	-

Vertebral Number

Yearling fish were X-rayed and vertebral numbers for 510 specimens were counted from photographic plates by means of transmitted light under a magnification of 4X. Results of these counts, showing means, standard errors and ranges, are shown in Figure 5. One group of 20 winter fish, to which reference was made earlier, exhibited malformed or fused vertebrae in 15 of the 20 specimens (75%). The mean and range in vertebral number for this group is shown at the top of Figure 5, but is not included in the statistical analysis.

The analysis of variance, presented in Table IV, indicates clearly the differences in vertebral counts, not only between the summer and winter stocks of fish, but also between groups of progeny from single females. The highly significant differences resulting from the between-stocks comparison substantiate the observations on wild, adult steelheads recorded in Tables I and II. In addition, a considerable degree of control of vertebral numbers in progeny appears to reside in each set of parent fish, as may be seen from the highly significant F values for the within-

stock comparisons, both for summer and for winter fish.

Figure 5. Number of vertebrae in F_1 summer and winter steelhead trout. Range is shown by the vertical bars at each end of the horizontal line for each sample. Standard error is shown as double horizontal line extending each side of the mean.

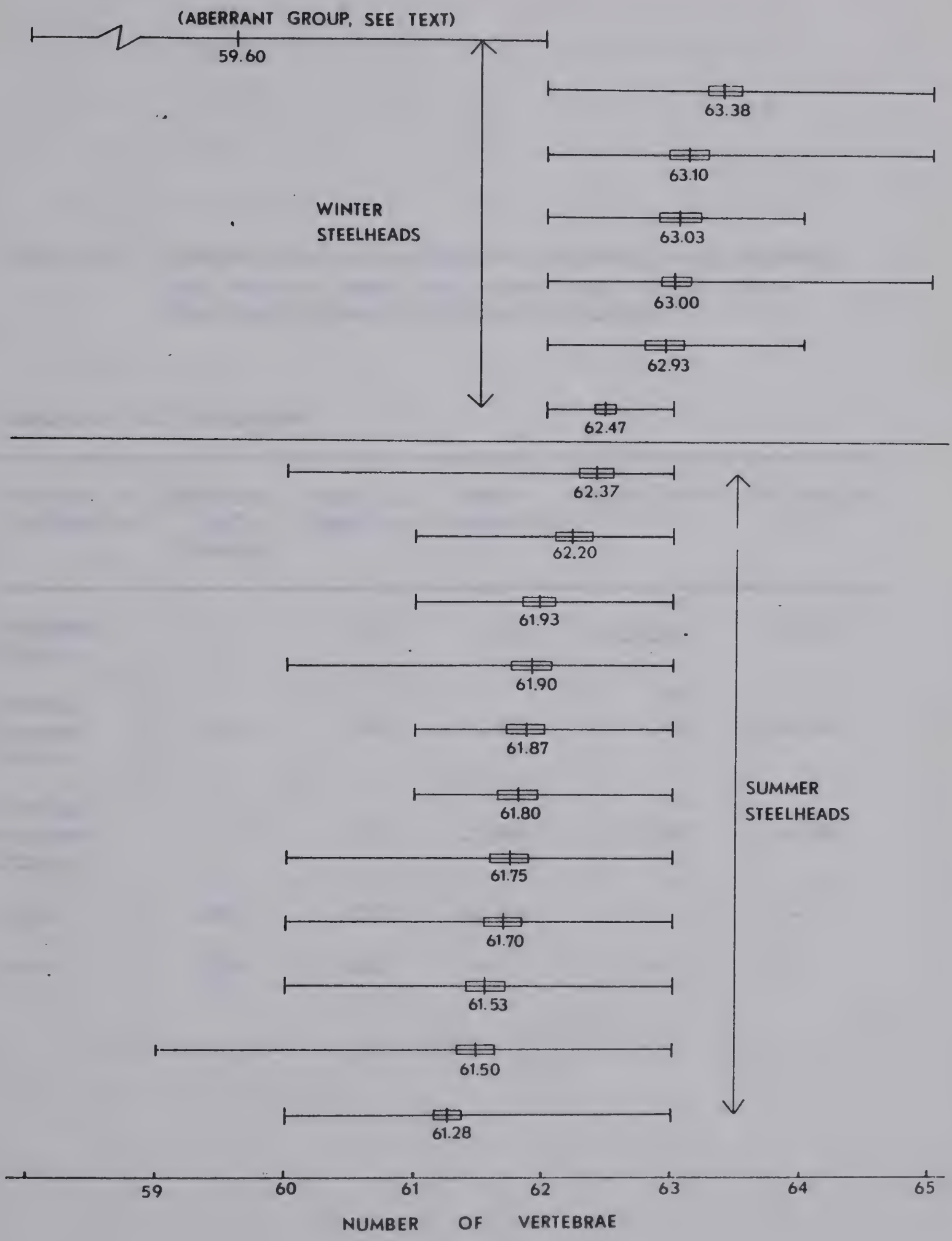

(ABERRANT GROUP, SEE TEXT)
59.60
63.38
63.10
63.03
63.00
62.93
62.47
WINTER
STEELHEADS
62.37
62.20
61.93
61.90
61.87
61.80
61.75
61.70
61.53
61.50
61.28
SUMMER
STEELHEADS
59
60
61
62
63
64
65
NUMBER OF VERTEBRAE

Table IV Comparison of vertebral counts in F_1 summer and winter yearling steelhead trout from Capilano River, British Columbia.

Analysis of Variance

Sources of Variation	Degrees of Freedom	Sums of Squares	Mean Squares	Calculated F	1% Table F
Between Stocks	1	172	172	390.90**	6.63
Within Summer Stock	10	33	3.30	7.50**	2.92
Within Winter Stock	5	13	2.60	5.91**	4.86
Error	492	218	0.44	-	-
Total	509	456	-	-	-

It may be seen from Figure 5 that the ranges in vertebral counts all overlap, but results of the analysis shown in Table IV indicate that on the basis of vertebral counts, summer and winter steelheads clearly can be assigned to separate populations ($P<0.001$). Grand averages for vertebral numbers in F_1 experimental fish are 61.82 and 62.99 for summer and winter stocks respectively. Of the total of 510 fish examined, 111 summer fish had vertebra numbers below the lowest number (62) recorded for winter fish, and 38 winter fish had vertebra numbers above the highest number (63) recorded for summer fish. Because all the yearling steelheads were reared under the same environmental conditions, the highly significant statistical difference in the vertebral numbers between and within these two stocks result from genotypic, rather than phenotypic effects. Similar data, presented earlier for wild adult fish from several rivers in British Columbia, can be viewed with considerable confidence, even if open to unknown environmental effects.

Gill Raker Structure

Early investigation of adult summer and winter

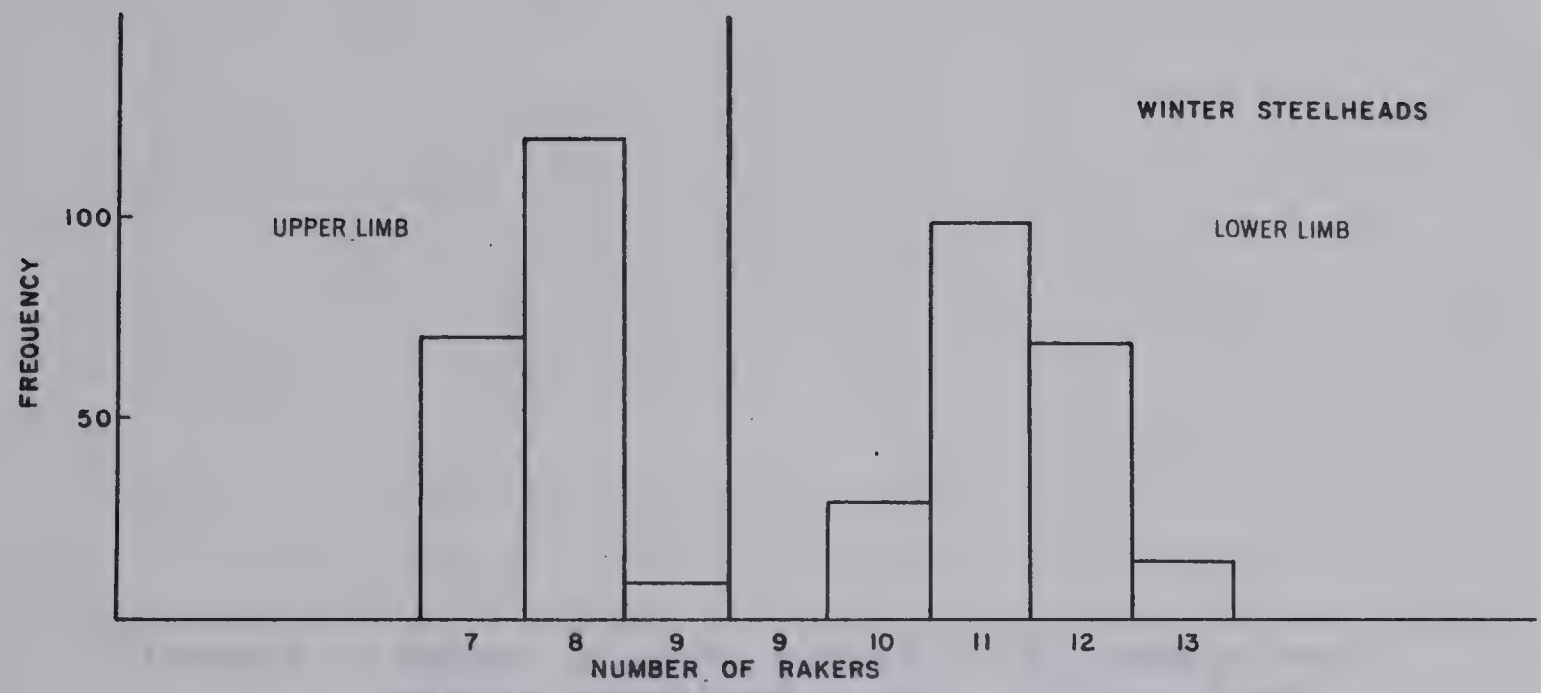
steelheads from Capilano River suggested that differences in gill raker structure might be important in separating these stocks. However, examination of Capilano River steelheads reared both in fresh and in salt water under environmental conditions which were the same for each stock, failed to reveal differences previously reported in wild fish (Smith, 1960). Smith had found flattening and bifurcation of gill raker tips in adult summer steelheads, but not in winter steelheads. Results in this study suggest that differences in gill raker structure reported earlier in adult steelheads are produced by unknown environmental effects.

Gill Raker Numbers

Gill raker counts were made on 510 yearling steelhead trout on the right anterior arch in all specimens. Counts for the upper and lower limb of the arch were made separately. Frequency distributions means and ranges of gill raker counts for yearling summer and winter steelheads are shown in Figure 6. Results of analyses for these data are summarized in Table V.

In these F_1 yearling steelheads, the ranges

in gill raker counts in the two stocks overlap almost completely, except that in the summer group one specimen was recorded with six rakers in the upper limb and three specimens with nine rakers in the lower limb, while in winter steelheads these counts for the respective limbs were not observed. Analyses of variance for the between-stock comparisons show that there are no statistically significant differences in <u>total</u> gill raker numbers between summer and winter steelheads. Summer steelheads however, have a significantly higher number of rakers in the upper limb and a significantly lower number in the lower limb of the gill arch than have winter steelheads ($P < 0.01$). For the within-stock comparisons, significant differences between groups of progeny in the summer stock occurred in upper limb counts and in the winter stock for lower limb counts ($P < 0.01$).


WINTER STEELHEADS
UPPER LIMB
LOWER LIMB
FREQUENCY
100
50
7
8
9
9
10
11
12
13
NUMBER OF RAKERS

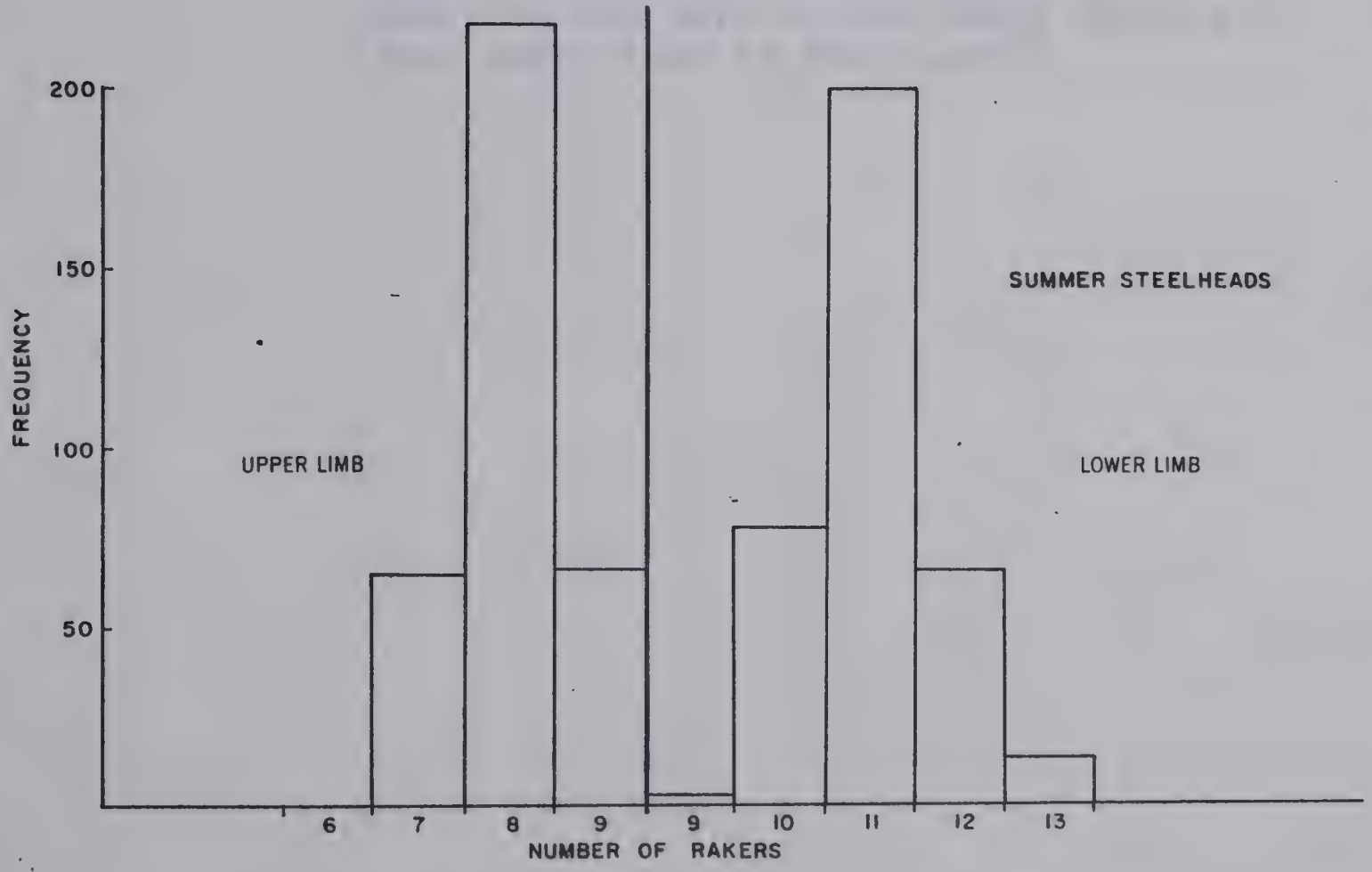

SUMMER STEELHEADS
UPPER LIMB
LOWER LIMB
FREQUENCY
200
150
100
50
6
7
8
9
9
10
11
12
13
NUMBER OF RAKERS

Figure 6. Number of gill rakers in F_1 summer and winter steelhead trout. (Upper limb counts to the left of the heavy vertical line, lower limb to the right.)

Table V Comparisons of gill raker numbers in F_1 summer and winter yearling steelhead trout from Capilano River, British Columbia.

A. Total gill raker numbers

Analysis of Variance

Source of Variation	Degrees of Freedom	Sums of Squares	Mean Squares	Calculated F	1% Table F
Between Stocks	1	0.11	0.11	0.12	39.86
Within Summer Stock	10	21.50	2.15	2.34	2.32
Within Winter Stock	5	19.39	3.88	4.21	4.10
Error	492	451.35	0.92	-	-
Total	509	488.91	-	-	-

cont'd..

Table V (cont'd.)

B. Gill raker numbers in upper limb of gill arch

Analysis of Variance

Sources of Variation	Degrees of Freedom	Sums of Squares	Mean Squares	Calculated F	1% Table F
Between Stocks	1	8.60	8.60	34.40	11.26
Within Summer Stock	10	15.19	1.52	6.08	3.80
Within Winter Stock	5	2.24	0.45	1.80	99.30
Error	492	123.67	0.25	-	-
Total	509	149.70	-	-	-

C. Gill raker numbers in lower limb of gill arch

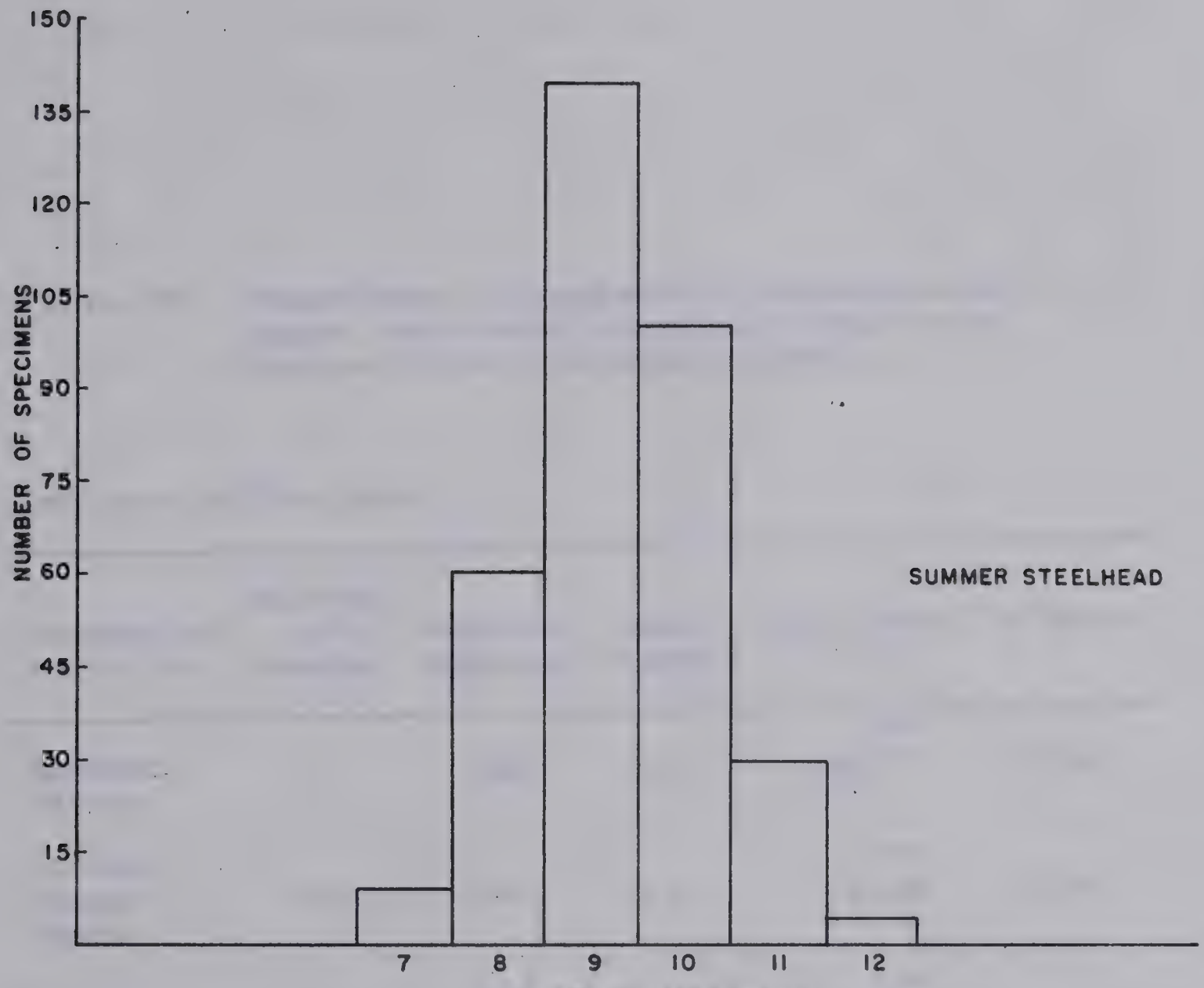
Analysis of Variance

Sources of Variation	Degrees of Freedom	Sums of Squares	Mean Squares	Calculated F	1% Table F
Between Stocks	1	10.00	10.00	20.41	10.04
Within Summer Stock	10	11.28	1.12	2.29	4.54
Within Winter Stock	5	13.38	2.68	5.47	4.86
Error	492	241.80	0.49	-	-
Total	509	276.46	-	-	-

Number of Parr-marks

Parr-marks were counted on 510 yearling F_1 steelheads from Capilano River stocks. Parr-marks were arbitrarily designated as any elongate pigmented areas on the side of the fish through which passed the lateral line. The distribution means and ranges of the number of parr-marks is shown in Figure 7. Statistical comparison of parr-mark counts in summer and winter fish is summarized in Table VI. As in the comparisons of vertebral, gill raker and scale counts, there was a tendency for individual females to produce progeny with a characteristic number of parr-marks. The variability in number of parr-marks, both in summer and winter steelheads is low, thus small differences in mean number are statistically significant. From Table VI it may be seen that highly significant differences occur between stocks as well as within both the summer and winter stocks.

Figure 7. Number of parr-marks in F_1 summer and winter steelhead trout.


150
135
120
105
90
75
60
45
30
15
NUMBER OF SPECIMENS
SUMMER STEELHEAD
7
8
9
10
11
12
NUMBER OF PARR MARKS

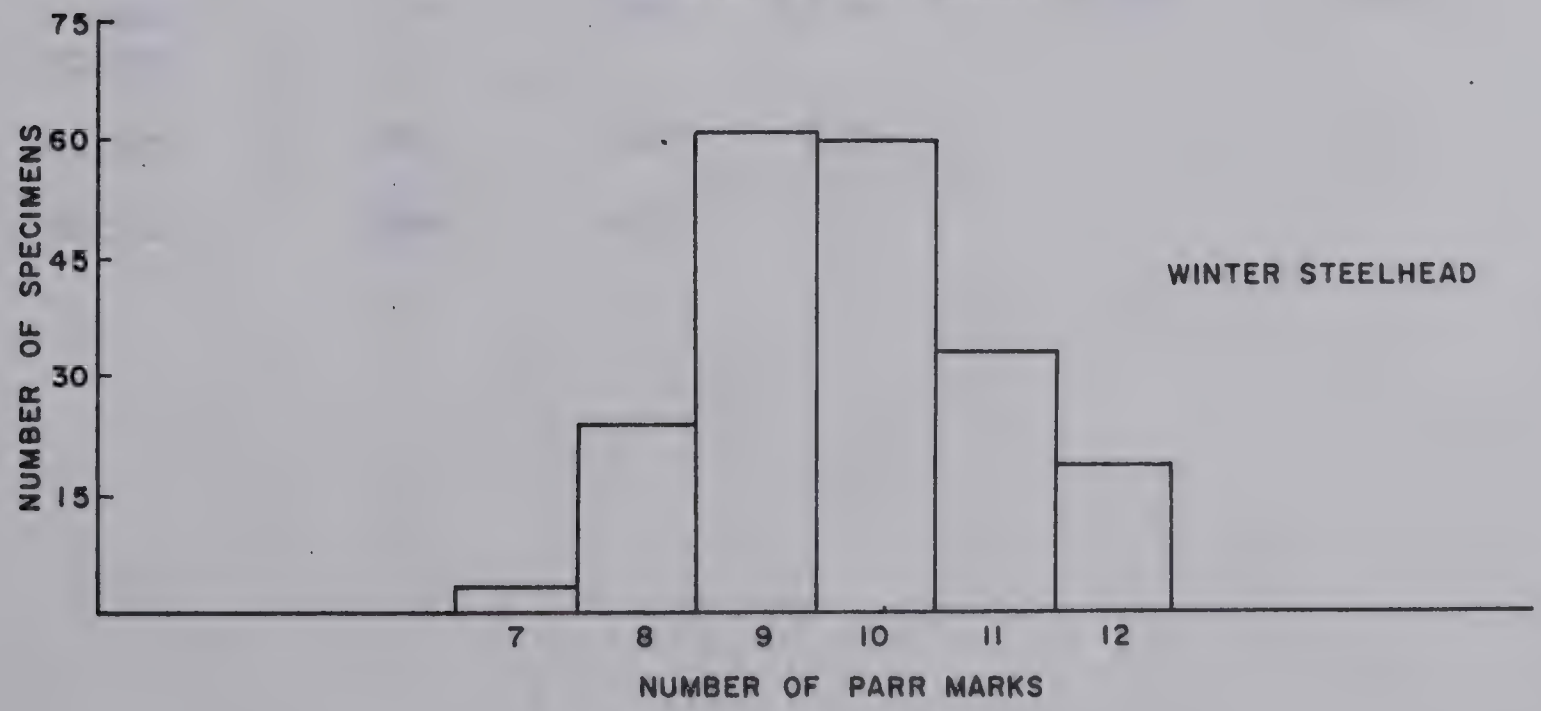

75
60
45
30
15
NUMBER OF SPECIMENS
WINTER STEELHEAD
7
8
9
10
11
12
NUMBER OF PARR MARKS

Table VI Comparisons of numbers of parr-marks in F_1 summer and winter steelhead trout from Capilano River, British Columbia.

Analysis of Variance

Sources of Variation	Degrees of Freedom	Sums of Squares	Mean Squares	Calculated F	1% Table F
Between Stocks	1	28	28	30.77**	7.64
Within Summer Stock	10	58	5.8	6.38**	2.63
Within Winter Stock	5	105	21.0	23.08**	3.02
Error	492	410	0.91	-	-
Total	509	601	-	-	-

Summary of Taxonomic Comparisons

Differences in taxonomic characters in F_1 summer and winter steelheads generally are small, but are in the same direction as those observed in parent fish. Further, in four meristic series (vertebrae, upper and lower limb gill rakers, parr-marks), differences were persistent enough that summer and winter steelheads raised under the same environmental conditions can be statistically assigned to separate populations. The evidence strongly supports the proposition that these stocks represent different genotypes, although variability is wide enough in all characters to preclude separation of individuals from the two stocks.

From the analyses of variance it is also apparent that many groups of progeny from single females tend to exhibit significantly less variability in numbers of vertebrae, gill rakers and parr-marks than the variability between progeny from different females.

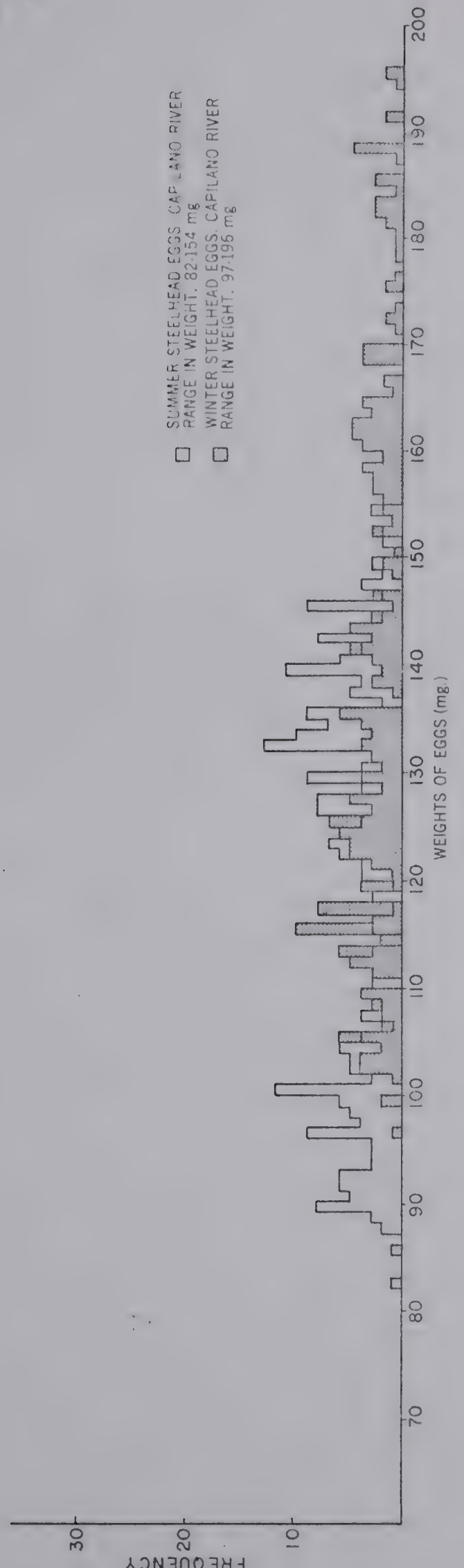
EGG SIZE IN STEELHEAD TROUT

Egg Size in Wild Steelheads

Samples of eggs were obtained from four populations of steelhead trout which had spent some time in the ocean: (1) wild Capilano River summer fish (2) wild Capilano River winter fish (3) Columbia River summer fish from Skamania, Washington and (4) winter fish from Chambers Creek near Tacoma, Washington. Columbia River summer steelheads and Chambers Creek winter steelheads, trapped during fish culture operations of the Washington State Game Department, were largely spawners which had returned from previous hatchery releases.

Duplicate measurements of egg diameters, made with a vernier caliper to the nearest 0.1 mm, revealed some variability in measurements of the same eggs. From samples of a minimum of 30 eggs from individual females, subsamples of 10 or more eggs were taken. On these latter eggs, weights to 1.0 mgm and diameters to 0.1 mm were recorded and diameters correlated with weights. Mean egg weights, mean egg diameters and the values for the correlation coefficients are given in Table VII. It is apparent

Figure 8. Weights of eggs in summer and winter steelheads from Capilano River, British Columbia, in summer steelheads from Skamania, Washington and in winter steelheads from Chambers Creek, Washington.


SUMMER STEELHEAD EGGS. CAPILANO RIVER
RANGE IN WEIGHT. 82-154 mg.
WINTER STEELHEAD EGGS. CAPILANO RIVER
RANGE IN WEIGHT. 97-195 mg.
FREQUENCY
WEIGHTS OF EGGS (mg.)

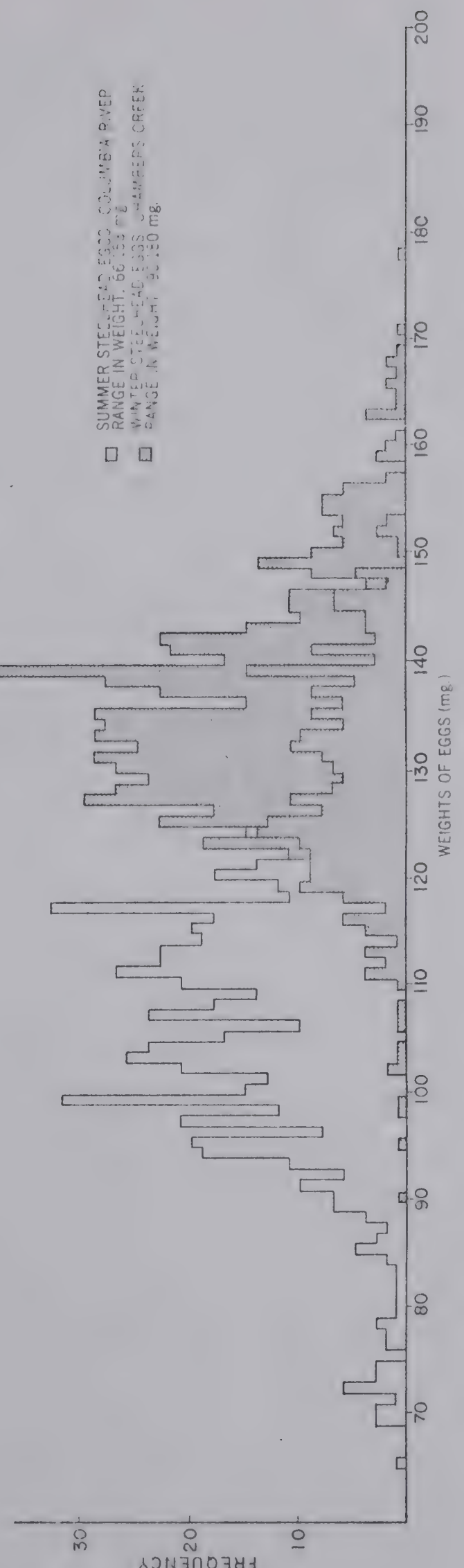

SUMMER STEELHEAD EGGS. COLUMBIA RIVER
RANGE IN WEIGHT. 66-154 mg.
WINTER STEELHEAD EGGS. CHAMBERS CREEK
RANGE IN WEIGHT. 90-180 mg.
FREQUENCY
WEIGHTS OF EGGS (mg.)

Figure 5. Number of vertebrae in F_1 summer and winter steelhead trout. Range is shown by the vertical bars at each end of the horizontal line for each sample. Standard error is shown as double horizontal line extending each side of the mean.

that some correlations are weak, suggesting that precision of measuring egg diamaters is not always satisfactory. All egg sizes were therefore determined by weighing eggs in subsequent samples.

Frequency plots of egg weights for the four population samples are shown in Figure 8. It will be noted that variability is much greater in egg size in Capilano River steelheads than in fish either from the Columbia River or from Chambers Creek. It is probable that variability in size of eggs has been reduced in Columbia River and Chambers Creek steelheads because of selection in hatchery operations. No clear separation of wild stocks of summer and winter steelheads can be made on the basis of egg size, although winter fish tend to have larger eggs than do summer fish.

Egg Size in Relation to Number of Vertebrae

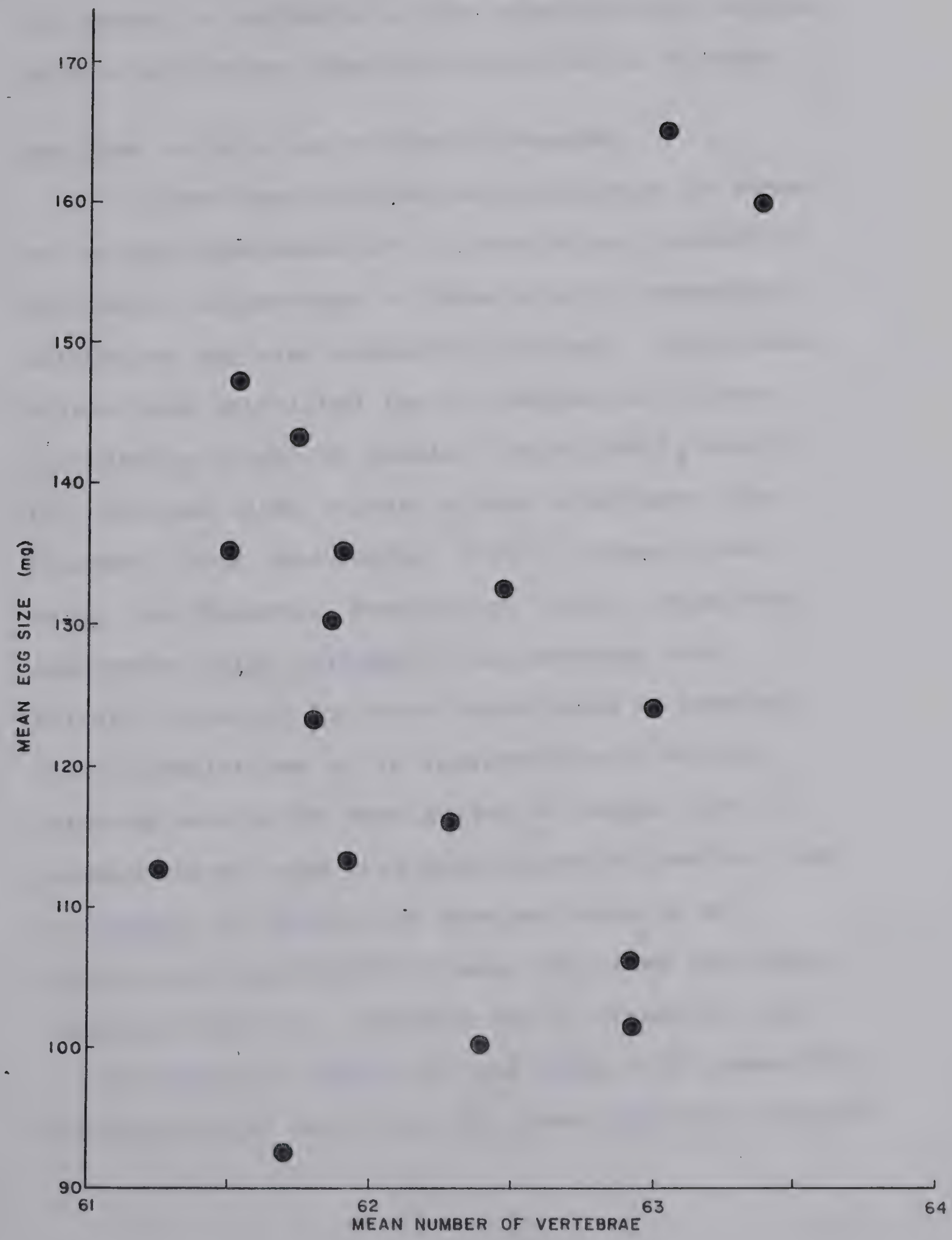
Significant statistical differences in vertebral counts appear to provide reasonable taxonomic criteria for separation of F_1 summer and winter stocks, but the possibility cannot be discarded that the long starvation of Capilano River summer steelheads resulted in a reduction in vertebral number in their progeny because these F_1 fish were hatched from smaller eggs.

Table VII Correlation coefficients calculated for the relation of egg diameters and egg weights in Capilano River summer and winter steelhead trout.

Number of eggs	Mean weight (mgm)	Mean diameter (mm)	Correlation coefficient	Probability level
11	96	4.2	0.49	$\geq$ 0.10
16	102	4.1	0.46	$\geq$ 0.10
10	104	4.3	0.58	$\leq$ 0.05
12	121	4.5		
10	126	4.3	0.56	$\leq$ 0.05
10	131	4.6	0.49	$\geq$ 0.10
12	143	4.6	0.57	$\leq$ 0.05
11	149	4.9	0.53	$\leq$ 0.05
13	161	5.1	0.61	$\leq$ 0.05

Lindsey (1962) discusses the possibility of correlation between egg size and meristic counts, citing Cartwright (1959), who found differences in egg size in anterior and posterior portions of ovaries in five species of freshwater fishes and Garside and Fry (1959), who reported a direct correlation between yolk mass and myomere count in some salmonids. Mean egg size (weight) was therefore plotted against mean number of vertebrae for 11 groups of summer steelheads and 6 groups of winter steelheads from Capilano River stocks. This plot is shown in Figure 9. Calculation of the correlation coefficient revealed no significant statistical relationship between egg size and number of vertebrae ($r=0.08$; $P>.10$).

Figure 9. Relation between mean egg weight and mean number of vertebrae in F_1 summer and winter steelhead trout.


170
160
150
140
130
120
110
100
90
MEAN EGG SIZE (mg)
61
62
63
64
MEAN NUMBER OF VERTEBRAE

For these groups of fish, it is apparent that the number of vertebrae is not significantly related to size of the egg from which the fish is hatched.

Egg Size in Relation to Size of Females

If persistent differences in egg size in summer and winter steelheads are to provide any indication of genetic differences in these stocks, phenotypic effects on egg size should be isolated. Correlation values were calculated for the regression of mean egg size on length of female, for F_1 and F_2 eggs of the Capilano River stocks; winter steelheads from Chambers Creek, Washington, U.S.A.; summer steelheads from Skamania, Washington, U.S.A.; from non-anadromous Salmo gairdneri from Kootenay Lake, British Columbia. In these comparisons of samples from 7 populations it is apparent that a strong tendency exists for populations of larger fish to produce larger eggs than populations of smaller fish but within the population samples there is no significant correlation of mean egg sizes with mean length of females. The data for F_2 steelhead eggs are presented in Figure 10, and Table VIII summarizes the statistical tests for the seven population samples.

Figure 10. Relation between mean egg weight and length of female in summer and winter steelhead trout raised to maturity in fresh water.

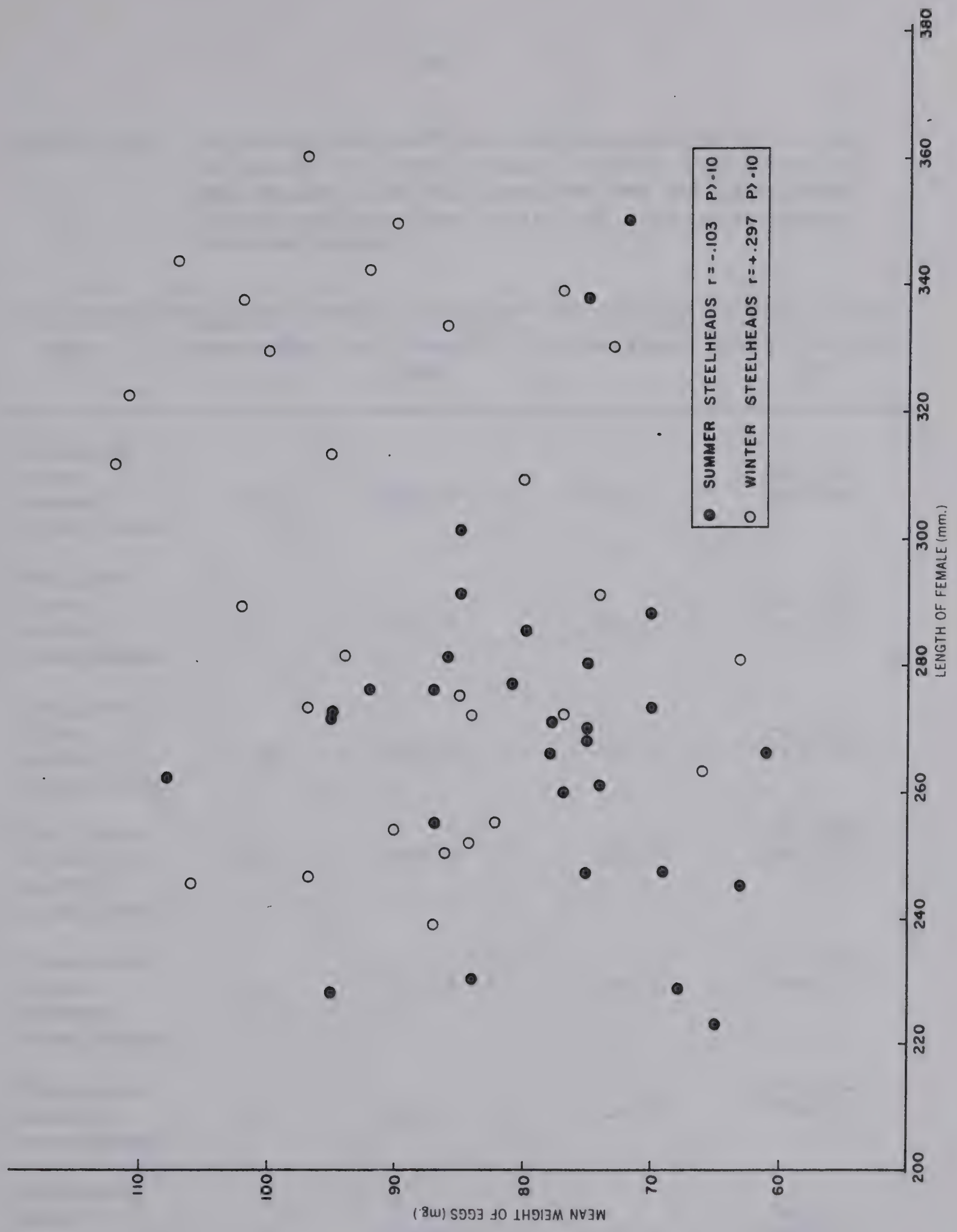

SUMMER STEELHEADS r=-.103 P>.10
WINTER STEELHEADS r=+.297 P>.10
MEAN WEIGHT OF EGGS (mg.)
110
100
90
80
70
60
LENGTH OF FEMALE (mm.)
280
300
320
340
360
380
260
240
220
200

Table VIII Correlation coefficients calculated for the relation of female mean lengths and means of egg weight for six populations of steelhead trout and one population of non-anadromous rainbow trout.

Source of eggs	Number of specimens	Mean length of female (mm)	Mean egg size (mgm)	Correlation coefficients (r)
Capilano River summer steelheads	11	658.0	121.5	+0.180 P>0.10
Capilano River winter steelheads	7	697.3	145.0	+0.201 P>0.10
Capilano River F_1 summer steelheads	30	269.5	79.2	-0.103 P>0.10
Capilano River F_1 winter steelheads	30	298.9	90.0	+0.297 P>0.10
Chambers Creek winter steelheads	26	673.6	138.3	-0.116 P>0.10
Skamania summer steelheads	30	623.1	114.6	+0.162 P>0.10
Kootenay Lake rainbow trout	25	752.8	151.4	+0.311 P>0.10

Egg Size in Experimental Populations

Eggs were obtained from F_1 progeny of Capilano River summer and winter steelheads, reared in fresh water from fertilization to yearling age at Cultus Lake Trout Hatchery and from yearling to maturity at Summerland Trout Hatchery, after transfer from Cultus Lake. All F_1 fish in each stock were exposed to the same environmental conditions from fertilization of eggs (May, 1960) until maturation in March, 1963. Samples of 30 eggs were taken from each of 30 females in these two experimental stocks, to provide F_2 eggs for comparisons between summer and winter groups. The sizes of eggs were compared by analysis of variance for differences in F_2 eggs produced by F_1 summer and winter fish. The pertinent statistical data are presented in Table IX, while Figure 11 shows the frequency distribution in sizes of the F_2 eggs.

It is apparent that the F_2 eggs in both stocks are much smaller than the F_1 eggs illustrated earlier in Figure 9. Range in egg size was reduced from 82-154 mgm to 55-114 mgm in summer steelheads and from 97-196 mgm to 53-122 mgm in winter steelheads. As mentioned earlier, significant correlations between egg size and length of female could not be demonstrated

in seven populations of S. gairdneri. When the data in Table VIII are plotted, however, as mean population egg sizes against mean population fish lengths (see inset on Figure 15), a strong tendency is shown for populations of larger females to produce larger eggs. The reduction in sizes of eggs produced by F_1 summer and winter steelheads can therefore probably be accounted for partly on the basis of size of females, which at maturity in fresh water were less than half the lengths of females from Capilano River, Skamania Hatchery or Chambers Creek.

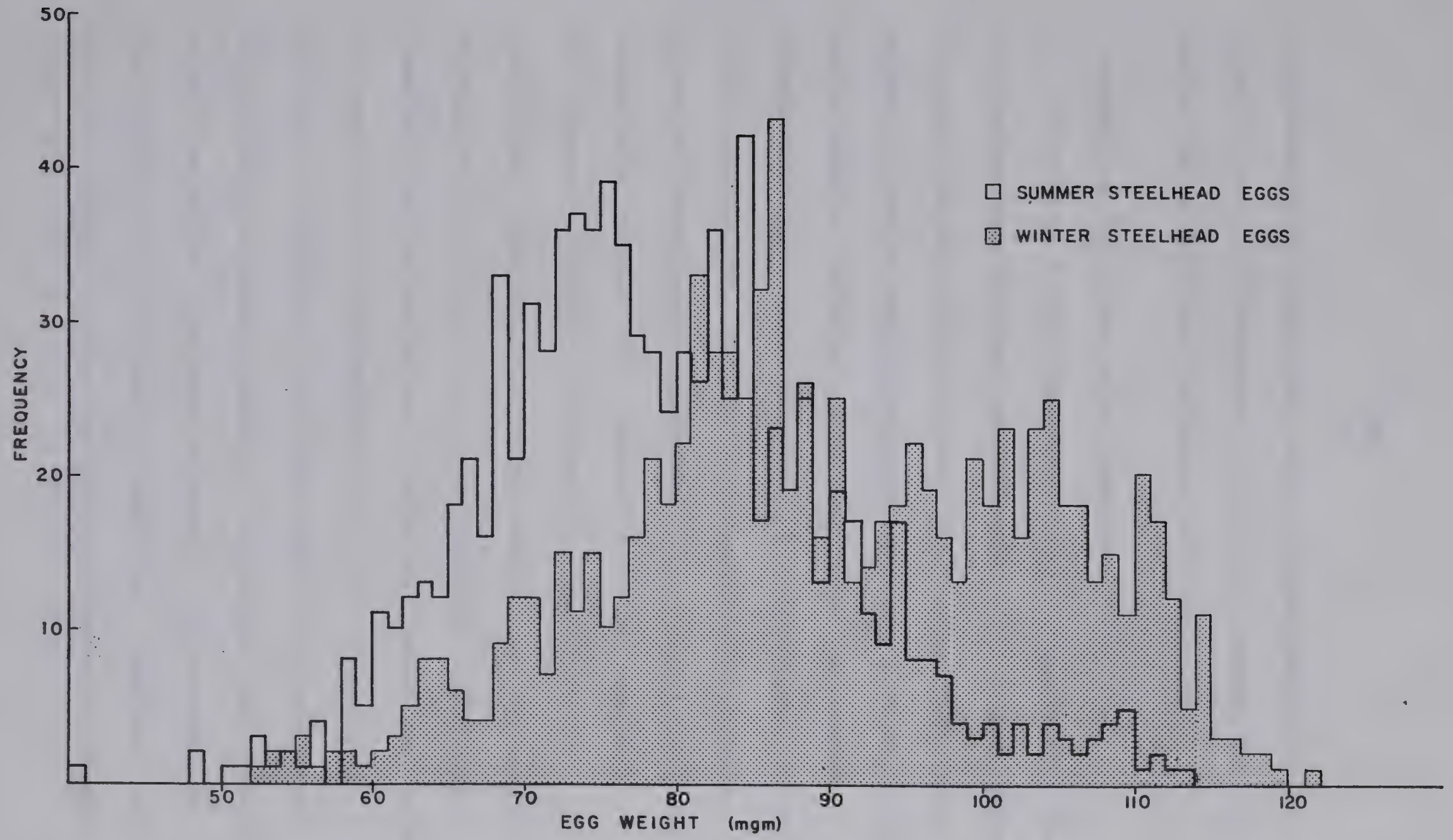
From the analysis of variance presented in Table IX, it is evident that egg size is strongly influenced by individual females within summer and winter stocks, and that variability in egg size between females is greater than that in eggs from individual females. With lack of significant correlation between egg size and length of females within populations, it would appear that genetic influence on egg size by individual females is strong enough to mask what seems to be a real tendency for populations of larger fish to produce larger eggs. In wild populations of summer and winter steelheads, starvation of summer fish during maturation could account for

Table IX Comparison of weights of F_2 eggs from Capilano River summer and winter steelhead trout raised to maturity in fresh water.

Analysis of Variance

Source of Variation	Degrees of Freedom	Sums of Squares	Mean Squares	Calculated F	1% Table F
Between Stocks	1	52,413	52,413	3,351**	6.63
Between females within summer stock	29	98,521	3,397	230**	1.69
Between females within winter stock	29	145,039	5,001	339**	1.69
Error	1,740	25,679	14.76	-	-
Total	1,799	321,652	-	-	-

Figure 11. Size of F_2 eggs obtained from summer and winter steelhead trout raised to maturity in fresh water.


SUMMER STEELHEAD EGGS
WINTER STEELHEAD EGGS
FREQUENCY
50
40
30
20
10
50
60
70
80
90
100
110
120
EGG WEIGHT (mgm)

differences in egg size, but in experimental F_1 populations, differences in egg size cannot be explained solely on the basis of fish size.

Summary of Egg Size Relationships

From the foregoing statistical comparisons the following conclusions may be drawn: (1) Differences in egg size between stocks of wild steelhead trout probably can be explained partially on the basis of environmental effects, where egg size in summer steelheads is reduced because of starvation during final maturation. (2) In F_1 experimental populations of steelheads, reduced F_2 egg size likely is associated partly with reduced size of females. (3) However, genetic influence on egg size by individual females is strong enough, and there is enough variability in egg size between individual females that correlation of size of female and size of eggs can not be demonstrated. (4) There is no evidence to suggest that any significant relationship exists between number of vertebrae and size of eggs from which fish are hatched. (5) Because of the control of egg size by individual females, and similar control of some meristic characters (Figure

5), extreme caution should be exercised in setting up experimental groups without adequate knowledge of the patterns of variability involved. An example may be seen in Figure 10. One female summer steelhead in this plot produced eggs with a mean weight of approximately 108 mgm, yet the fish was only 260 mm long. A winter female with a length of 330 mm produced eggs with a mean weight of only 73 mgm. If only one summer and one winter fish had been used to produce experimental F_1 progeny, it appears that the probability would have been large to obtain progeny which were not representative of the two populations.

MATURATION CHARACTERISTICS IN EXPERIMENTAL FISH

Gonad development in summer and winter steelheads from Capilano River stocks was examined in fish from ages I to III in fresh water and from ages I to IV in salt water. Several hundred summer and winter fish were examined at the Fish and Game Branch trout hatchery at Summerland, British Columbia from May, 1961, when they were transferred from Cultus Lake Hatchery as yearlings until they matured in March, 1963. Temperature of the water at Summerland was constant at 10.6^0 C (51^0 F). Similar groups of

yearling-plus steelheads were transferred from Cultus Lake Hatchery in August, 1961 to salt water rearing facilities at the Pacific Biological Station of the Fisheries Research Board of Canada at Nanaimo, British Columbia. All of the winter fish and three of the summer fish matured in the salt water environment by March, 1964, when the remaining specimens were killed and preserved for future examination. Temperature of the salt water at Nanaimo was variable between 6.2° C and 15.7° C during the time fish were held at that station.

Samples of fish were taken at intervals from both the fresh and salt water environments. Fish reared in salt water grew larger than their siblings held in fresh water, but comparisons of rates of growth in the two environments has no precise meaning because of the differences in physical dimensions of holding tanks, in diet and in temperature conditions. Within each environment, however, individuals from the two stocks provided specimens which, with respect to maturation characteristics, could be compared directly. From these comparisons were deduced the degree of genetic separation of the two stocks. Comparisons of maturation rates

were made for both sexes in each environment, but comparisons of the number and size of eggs produced were not made for fish which matured in salt water, because only one female and two males of the summer stock matured, from a total of 139 summer fish examined from the salt water environment.

Study of the maturation of summer and winter steelheads in controlled environments is complicated by the chronology of natural gonad development of wild fish of the two stocks. In Capilano River, for example, summer and winter steelheads ascend the river from the ocean in part at least, at the same time of year (Smith, 1960). Thus, summer fish captured in May, 1959, and which provided the parent summer stock for these experiments, had to be held until May, 1960, when gravid, late winter fish were also available. At that time, members of both strains were artificially spawned and the resulting progeny were from that time onward, reared under the same environmental conditions.

Gonad Development in F_1 Steelheads in Fresh Water

Because of wide differences in size of fish, maturation rates can best be examined from compari-

sons of the unit gonad weight per unit of body weight in individual specimens. For yearling fish, the relation of gonad weight to body weight is shown in Figures 12 and 13. The regressions were calculated from the combined values for 11 groups of males and 11 groups of females for the summer stock and 7 groups of males and 7 groups of females for the winter stock. Each of the 18 groups represents a set of 30 progeny from a single female parent. Variability in the gonad/body relationship of male steelheads is much greater than in females, and no significant regression of gonad weight on body weight could be demonstrated for male yearling steelheads. Female summer steelheads showed a tendency to have slightly larger gonads than comparable female winter steelheads, but the slopes of the regressions of gonad weight on body weight in the two stocks were not significantly different. A recapitulation of the regression plots for the gonad/body relation of female yearling steelheads is shown for comparison with other plots on Figure 14.

Figure 12. Relation between gonad weight and body weight in F1 yearling summer steelhead trout.

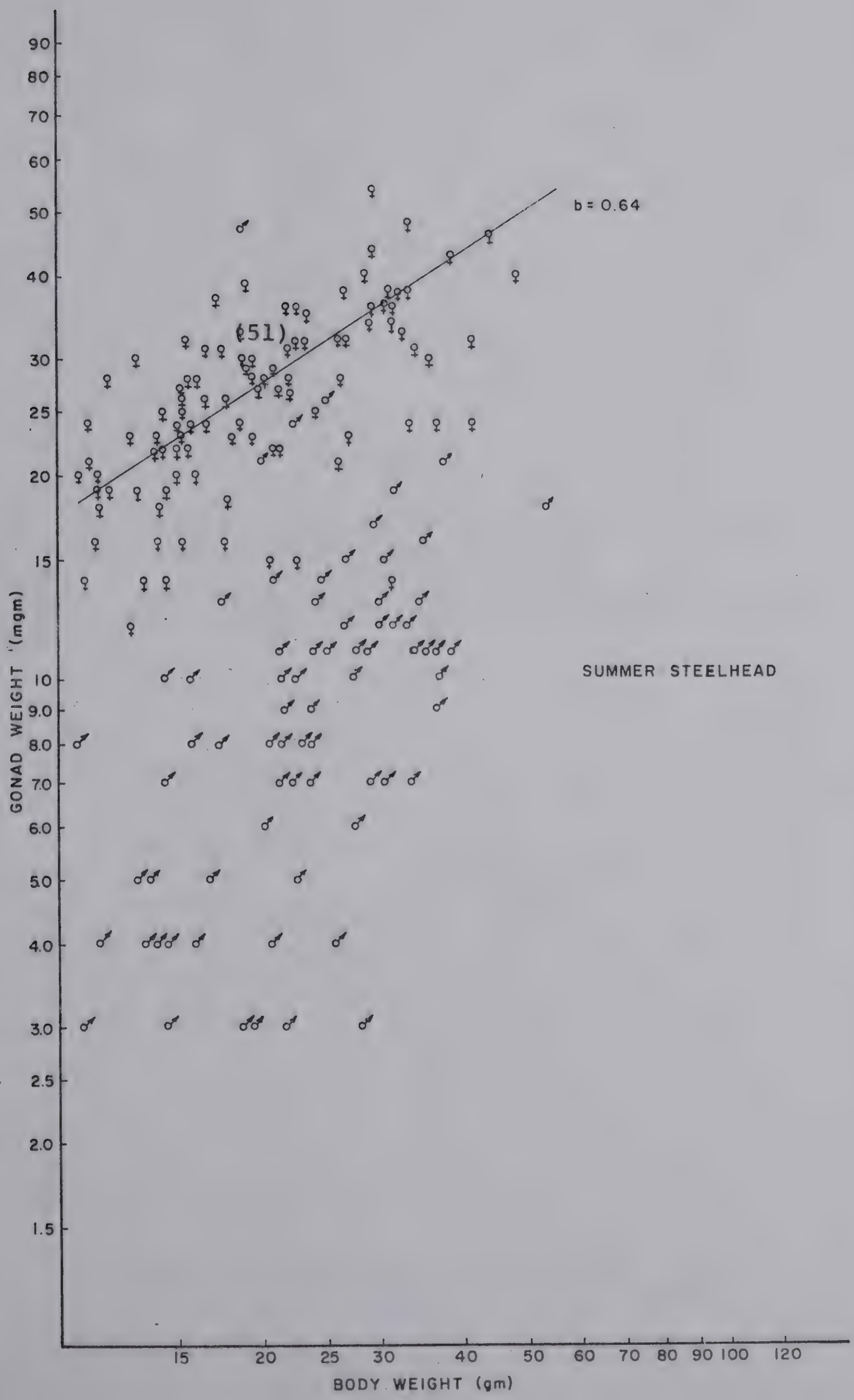

b = 0.64
(51)
SUMMER STEELHEAD
GONAD WEIGHT (mgm)
BODY WEIGHT (gm)
90
80
70
60
50
40
30
25
20
15
10
9.0
8.0
7.0
6.0
5.0
4.0
3.0
2.5
2.0
1.5
15
20
25
30
40
50
60
70
80
90
100
120

Figure 13. Relation between gonad weight and body weight in F_1 yearling winter steelhead trout.

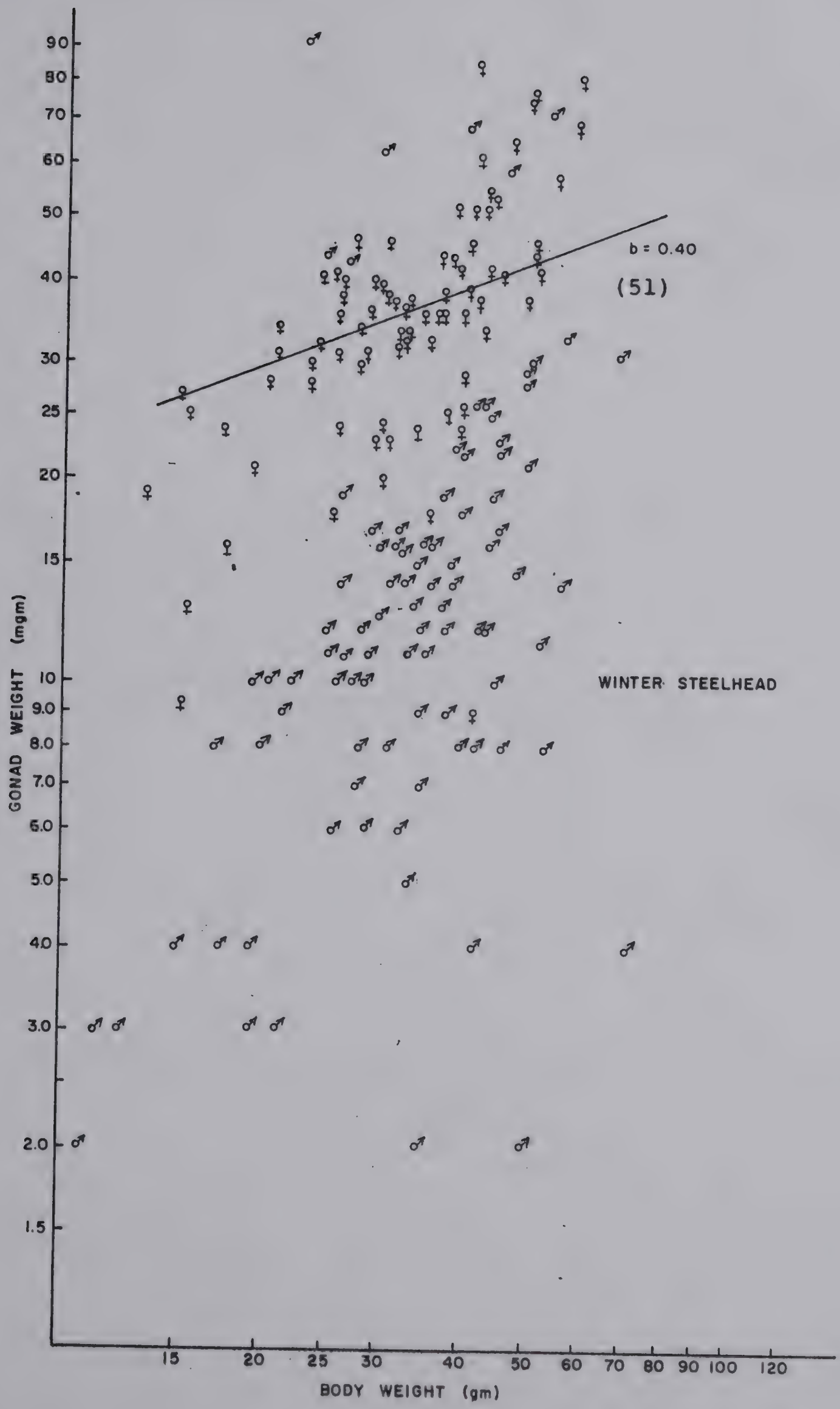
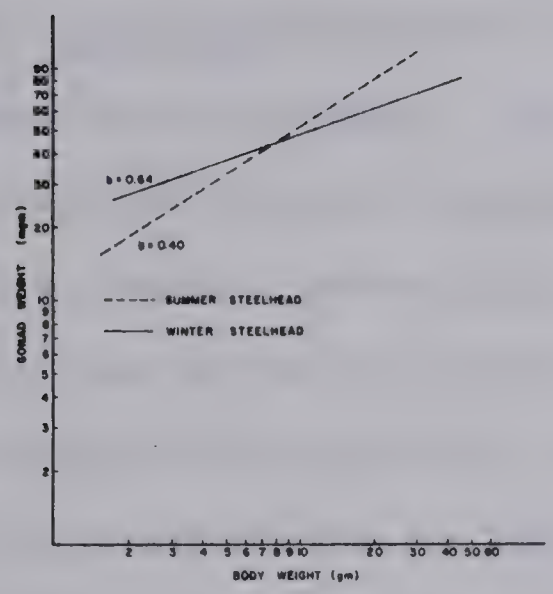
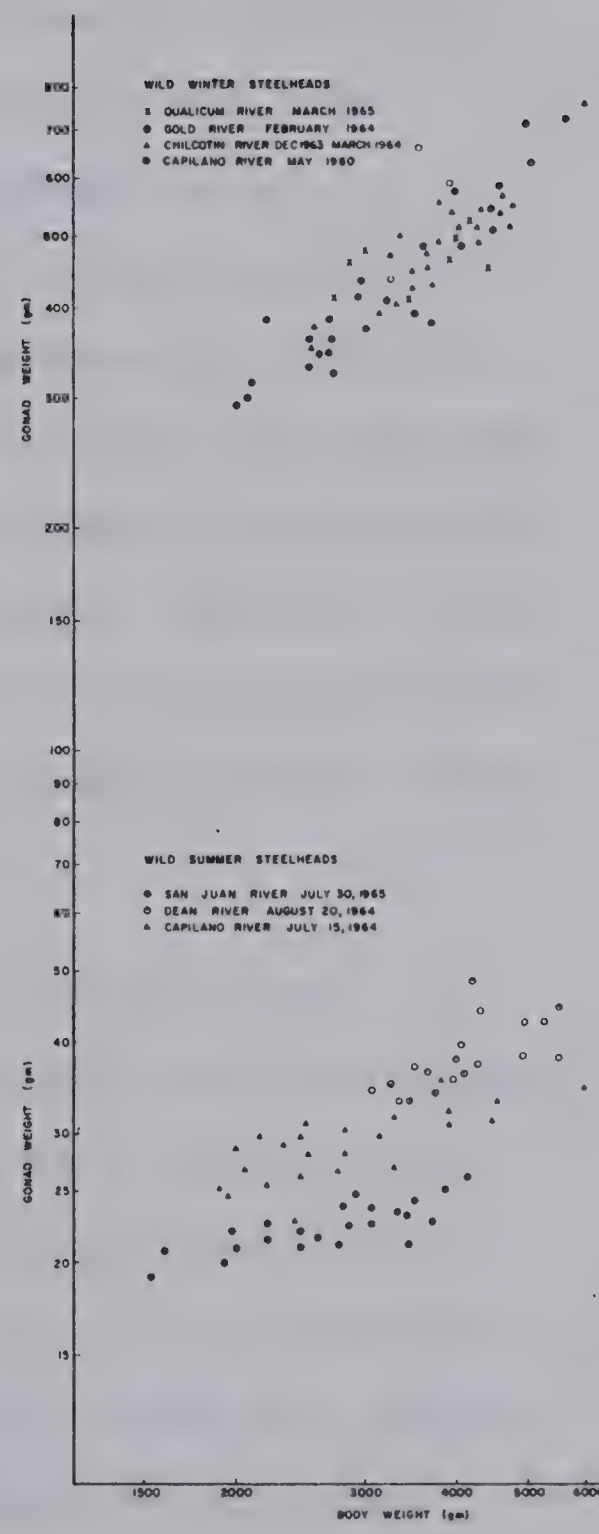
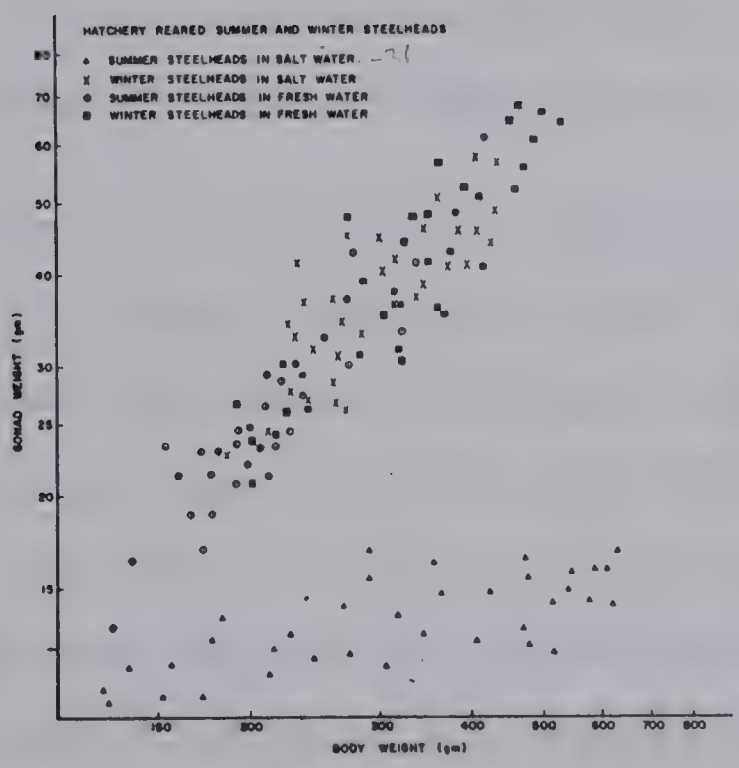

b = 0.40
(51)
WINTER STEELHEAD
GONAD WEIGHT (mgm)
90
80
70
60
50
40
30
25
20
15
10
9.0
8.0
7.0
6.0
5.0
4.0
3.0
2.0
1.5
15
20
25
30
40
50
60
70
80
90
100
120
BODY WEIGHT (gm)

Figure 14. Relation between gonad weight and body weight in over-yearling F_1 summer and winter steelhead trout reared in fresh and in salt water, and in wild summer and winter steelhead trout captured from six British Columbia streams. A recapitulation of the regressions from Figures 12 and 13 (females only) is shown for comparison on the upper left side of the figure.


GONAD WEIGHT (mgm)
b = 0.64
b = 0.40
SUMMER STEELHEAD
WINTER STEELHEAD
BODY WEIGHT (gm)


WILD WINTER STEELHEADS
QUALICUM RIVER MARCH 1965
GOLD RIVER FEBRUARY 1964
CHILCOTIN RIVER DEC 1963 MARCH 1964
CAPILANO RIVER MAY 1960
GONAD WEIGHT (gm)


HATCHERY REARED SUMMER AND WINTER STEELHEADS
SUMMER STEELHEADS IN SALT WATER
WINTER STEELHEADS IN SALT WATER
SUMMER STEELHEADS IN FRESH WATER
WINTER STEELHEADS IN FRESH WATER
GONAD WEIGHT (gm)
BODY WEIGHT (gm)

WILD SUMMER STEELHEADS
SAN JUAN RIVER JULY 30, 1965
DEAN RIVER AUGUST 20, 1964
CAPILANO RIVER JULY 15, 1964
GONAD WEIGHT (gm)
BODY WEIGHT (gm)

From Figures 12 and 13 it may be seen that no significant difference exists in the gonad/body-weight relationship of populations of summer and winter yearling steelheads reared in the same freshwater environment. The production of reproductive tissue in females in both stocks of fish is however, about twice as much per unit body weight than it is for males. As these fish approached maturity in fresh water (Figure 14) the relationship of gonad weight to body weight continued to be somewhat variable, but no marked difference existed in the gonad/body-weight relationship between stocks, even when fish became gravid.

Egg Production During Freshwater Maturation

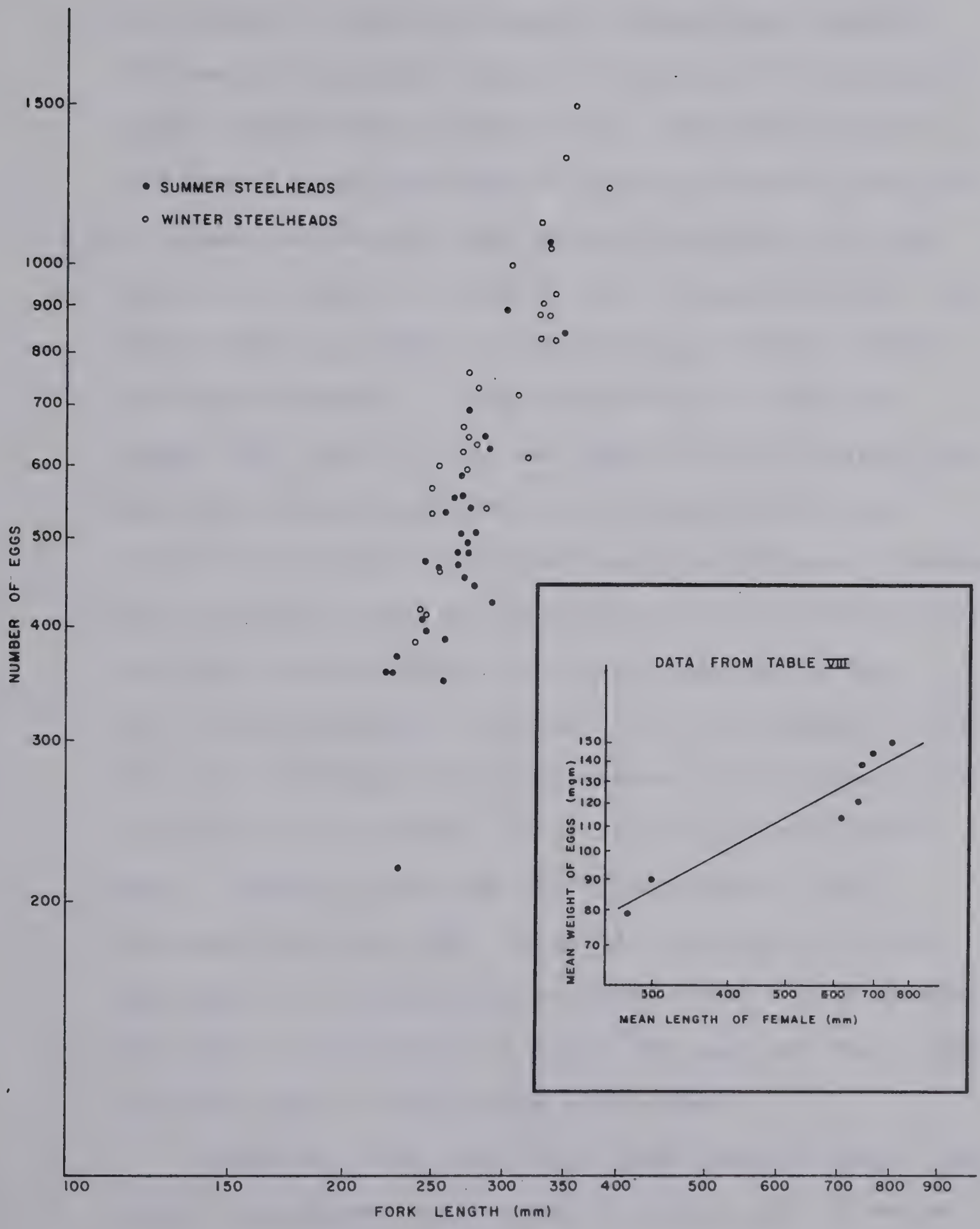
Winter fish as fry were longer than were summer fish, principally because they were hatched from larger eggs, and this size difference persisted throughout the life of the fish. As a consequence, winter females were considerably larger than summer females at maturity. Winter females had a mean length of 299 mm and produced an average of 790 eggs each. Summer females had a mean length of 270 mm and produced an average of 518 eggs each. The

relation between lengths of females and numbers of eggs produced is shown for each stock in Figure 15. There was no significant difference in the slopes of the regression of egg number on fish length between the two stocks ($P > 0.05$).

In summary, individual females of the F_1 generation of both summer and winter steelheads exert persistent genetic control over the size of individual eggs produced, while number of eggs is largely determined by length of fish. Data available from another, independent study on a population of non-migratory S. gairdneri from Kootenay Lake, British Columbia (Smith and Stringer, unpubl.) strongly indicates that a similar relationship of control of egg size and number exists in that population also.

Viability of Eggs From Steelheads Matured in Fresh Water

Mortality of F_2 eggs obtained from each of the two (F_1 summer and winter) steelhead stocks was recorded from fertilization to hatching. Loss was much higher in eggs from both summer and winter steelheads matured in fresh water than it was in


• SUMMER STEELHEADS
○ WINTER STEELHEADS
NUMBER OF EGGS
1500
1000
900
800
700
600
500
400
300
200
100
150
200
250
300
350
400
500
600
700
800
900
FORK LENGTH (mm)
DATA FROM TABLE VIII
MEAN WEIGHT OF EGGS (mgm)
150
140
130
120
110
100
90
80
70
300
400
500
600
700
800
MEAN LENGTH OF FEMALE (mm)

eggs obtained from steelheads which had matured in salt water or which had spent a significant period of time in the ocean (Capilano River wild winter and summer steelheads respectively). The mortalities in artificial fertilizations of F_2 eggs from 60 pairs of F_1 summer and winter fish matured entirely in fresh water are listed in Table X. It is apparent that the mortalities in summer and winter eggs are not significantly different. From these data it could be argued that size of fish and mortality were associated, since wild steelheads were much larger than those reared to maturity in the hatchery facilities. However, fish culture operations carried out by British Columbia Fish and Wildlife Branch hatchery personnel often utilize non-migratory rainbow trout of a smaller size than the steelheads discussed above, with mortalities of less than 10 percent in artificially fertilized eggs. Average loss from fertilizations of wild steelhead eggs was 18%. Probably mortality of eggs from fish reared entirely in fresh water is associated with lack of exposure, at least for part of their life, of these fish to the marine environment.

Cross fertilizations were made between summer and winter steelheads, utilizing 10 females and 10 males

Table X Mortalities in eggs from summer and winter steelhead trout brought to maturity in fresh water.

Source of eggs	Number of females	Total eggs	Mean number eggs/female	Mean loss (percent)	Value of "t"
Summer steelheads	30	15,540	518	62.9	1.08 P>0.10
Winter steelheads	30	23,728	791	72.3	

from each stock. Mortality in crosses between strains was compared with mortality in fertilizations within strains, in order to assess the degree of genetic compatability between stocks. Reciprocal crosses resulted in viability of eggs no different than that obtained for within-strain fertilizations. Thus, any differences in survival of eggs in the cross-fertilizations appear to result from factors other than genetic incompatability.

Summary of Maturation Experiments

Winter steelheads produced a larger number of eggs per female than did summer fish (Table X), but this was a phenotypic, rather than a genotypic effect (Figure 15). When a significant portion of the life of the fish had been spent in salt water, mortality of eggs was low and did not differ significantly between the two strains. Where the entire life of the fish had been spent in fresh water, mortality of eggs from all fish was high, but not significantly higher in winter than in summer fish. It may be concluded therefore, that parental history and egg mortality were not associated when the fish were reared entirely in fresh water.

Gonad Development in Salt Water

Samples of fish from the F_1 Capilano River summer and winter stocks, reared together in salt-water facilities at Nanaimo, British Columbia indicated that maturation characteristics of each group in a saltwater environment are strongly heritable. During three years of residence in salt water, gonads of winter fish developed at a rate similar to that observed for both summer and winter steelheads in fresh water. The rate of gonad development in summer steelheads reared in sea water was however, much lower than in winter fish. Of all specimens examined (65 summer and 67 winter fish) all winter fish, but only three of the summer steelheads showed significant gonad development. All fish at Nanaimo were four years of age when the experiment was concluded. The data are presented in Figure 14. It should be mentioned that the three summer fish which matured could have been mistakenly marked before transfer to salt water, since jumping of yearling fish between pens in the holding troughs was detected after fish had been fin-clipped. It is not known whether a period of residence in fresh water is essential for maturation

of summer fish. However, three adult, but sexually immature summer steelheads transferred in 1959 from Capilano River fish traps three miles above tidal influence to saltwater facilities at the Vancouver Public Aquarium showed no external evidence of sexual maturation up to 18 months later.

MATURATION IN NATURE

Comparisons of egg production in summer and winter steelheads cannot be made without considering environmental effects which may act on physiological processes during final maturation. During final maturation of gonads in nature, winter steelheads are in salt water and summer steelheads are in streams. Further, summer steelheads do not consume significant quantities of food during the maturation period, while winter fish at least have food available in the ocean, although it is not known to what extent they may feed during the maturation period. Summer steelhead have been held for as long as 12 months in freshwater hatchery facilities without food and with little evidence of high egg mortality when spawned (Smith, 1960).

Atresia in Ovaries of Wild Steelheads

Evidence is available to indicate the condition of ovaries of both summer and winter steelheads which have matured under natural conditions. Complete gonads of 17 female winter steelheads from Qualicum River, 23 winter females from Chilcotin River, 10 winter females from Capilano River, 21 summer females from Dean River, 11 summer females from San Juan River and 23 summer females from Capilano River were examined. The percentage of follicular atresia (reabsorbed eggs) was determined for each female by gross examination of ovaries. Summer fish from Dean and San Juan Rivers were captured only a short time after they had left the ocean, but it is not known how long winter fish from Qualicum, Chilcotin and Capilano Rivers had been in those streams. Data concerning follicular atresia are summarized in Table XI.

Figure 15. Relation between length of female and number of eggs in F_1 summer and winter steelhead trout reared to maturity in fresh water.

Table XI Follicular atresia in ovaries of steelhead trout from six British Columbia streams.

Stock	Source of fish	No. of fish	Level of maturation	Mean Number of eggs Atretic	Mean Number of eggs Normal	Mean % atresia	Probable time in stream
Summer	Dean River	21	Immature	417	3,963	9.5	1 week
Summer	San Juan River	11	Immature	218	2,871	7.6	1 week
Winter	Chilcotin River	23	Mature	608	4,321	12.3	2 months
Winter	Qualicum River	17	Mature	590	3,405	14.7	1 month
Summer	Capilano River	23	Mature	2,601	2,112	55.1	10 months*
Winter	Capilano River	10	Gravid	687	3,012	18.5	1 month

* Time spent in fresh water known within one week.

From Table XI it may be seen that the level of follicular atresia was low in Dean River and San Juan River summer steelheads a short time after these fish had left salt water. Further, the level of atresia in mature winter fish from Chilcotin, Qualicum and Capilano Rivers also was low. Mature summer fish from Capilano River, examined 10 months after these fish had left the ocean, showed an atresia rate of more than 50 percent. Three specimens of summer steelheads captured in February, 1965 from San Juan River, showed atresia rates of 73, 66 and 59 percent. The latter of these specimens was tagged on August 2nd, 1964 and was recaptured on February 14th, 1965, after 196 days in the river. The tagged fish had no food in its stomach, the walls of which were pressed so closely together that there was no discernable lumen.

Because of the lack of certainty concerning length of residence in spawning streams, statistical comparisons of atresia in the six population samples was not attempted. However, the low levels of atresia in the ovaries of summer fish which had been in streams only a short time (Dean and San Juan Rivers) and the very high levels in summer fish which

had been in Capilano and San Juan Rivers for an extended period, strongly suggest that prolonged starvation markedly increases the rate of follicular atresia in steelheads when the ovary is not fully developed before the fish leaves the ocean. A similar situation was demonstrated experimentally by Scott (1962) for non-anadromous S. gairdneri, reared under controlled conditions of diet. Field data presented in that study suggested that reduced stomach volumes in late summer in lake-resident rainbow trout was associated with follicular atresia. Scott states in part ". . . starvation reduces the number of eggs brought to maturity through the mechanism of follicular atresia." It should be stressed that follicular atresia as observed in the present investigation is concerned with the gross aspects of the phenomenon, and takes into account only those atretic eggs which can be observed under relatively low magnification (X30). Further, the total number of eggs observed in each specimen does not necessarily represent the full complement of eggs laid down originally in the embryonic ovary. Detailed histological examination of ovarian tissues would be required to demonstrate adequately the total

atretic process from oogenesis to full maturation. Nevertheless, the data presented herein illustrate clearly enough that as a result of sharply different, genetically controlled patterns of maturation physiology, environmental factors during final maturation of ovaries can exert strong effects on the relative fecundity of these two stocks of fish.

Gonad Development

Summer and winter strains of steelheads both exhibit considerable variability in life history patterns (Withler, 1966) and comparisons of gonad development may be complicated by size of fish, which may spend from one to three years in salt water. In view of the foregoing, statistical analyses were not employed to compare the gonad/body-weight relationships in population samples from Gold, San Juan and Qualicum Rivers on Vancouver Island and Dean, Capilano and Chilcotin Rivers on the mainland of British Columbia. Data for gonad/body plots of seven population samples of wild steelheads are shown in Figure 14.

An important relationship in gonad development of the two stocks of steelheads may be

deduced from Figure 14. Summer and winter steelheads raised under the same environmental conditions are easily separable on the basis of gonad development in salt water. Winter steelheads raised in salt water (Figure 14) have much larger gonads at any fish size than summer fish raised in salt water. Gonad/body plots of winter steelheads captured during their migration from salt water in Gold, Qualicum and Chilcotin Rivers show substantially the same gonad/body proportion as that observed for winter steelheads reared in sea water at Nanaimo. Development of gonads in relation to increase in body weight appears to be reasonably linear in wild winter steelheads, as well as in winter steelheads reared in a controlled environment.

When wild summer steelheads from San Juan and Dean Rivers are compared to summer steelheads reared at Nanaimo, the slope of the gonad/body plot appears to be increased in the larger wild specimens, suggesting that a positive inflection has occurred in the gonad/body-weight growth curve of these fish during their residence in the freshwater stream environment. On entry to fresh

water from the ocean, summer steelheads generally are as large as winter adults but are sexually immature on entrance to spawning streams. On the other hand, it should be stressed that while final maturation of gonads is proceeding in fresh water, no body growth occurs, and maturing summer steelheads may lose weight (Table XII, Fig. 16). Thus the relationship which is evident in all other gonad/body plots does not obtain during the final maturation period for summer steelheads.

Weight Loss During Maturation

When comparing the gonad/body-weight ratios of wild fish, it is important to consider that the whole maturation history of the fish is not available for wild specimens, but can only be deduced from chronological events during maturation. When the total number of fully developed eggs has been determined, the weight of the ovary probably will not shift greatly. However, evidence is available from summer fish in San Juan River that the body weight of individuals in this population decreased during prolonged residence in fresh water. During July and August, 1964, 112 summer steelheads were

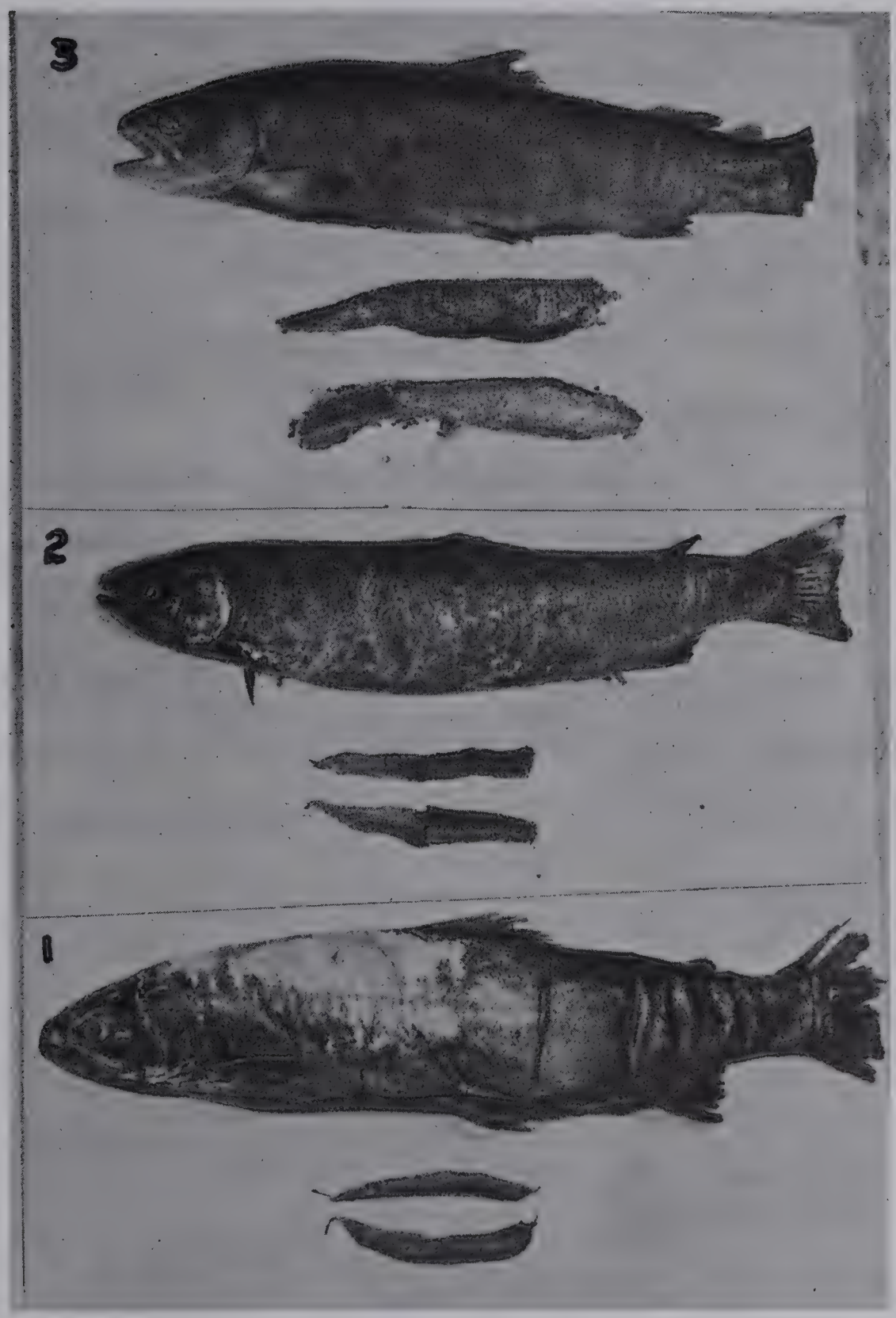
tagged and released to proceed upstream. All of these fish were weighed prior to release. During the late summer, autumn and winter of 1964-65, 15 of the tagged fish were reported by anglers and the tags returned. Of the 15 specimens reported, weights were noted for 6 female fish. Although there is no way of checking the accuracy of the scales used by the anglers to weigh the fish, all specimens reported were lighter than the weights recorded at the time the fish were tagged. The date of tagging, date of reported capture, weight at time of tagging and weight at time of recapture by angling are shown for the six specimens in Table XII. It will be noted that one fish was reported at a weight 26 percent less than its weight 177 days previous, and that the average weight loss was in excess of 17 percent.

During August, 1965 summer steelheads were trapped in San Juan River. Of a total of 38 fish captured, 12 were killed at the time of entry to the fish traps and 26 were transported to the Fish and Game Branch Hatchery near Abbotsford, where they were held in a natural outdoor pond. A male and a female were killed each 14 days for samples. Temperature of the water at Abbotsford Hatchery is 11^{o} - 12^{o} C

Table XII Weight loss in female summer steelhead trout during maturation in San Juan River, British Columbia.

Date tagged	Date of recapture	Days in river	Weight when tagged (kg)	Weight at recapture (kg)	Percent loss in weight
July 28/64	Jan.10/65	168	5.22	4.72	10
Aug. 2/64	Jan.11/65	162	4.45	4.00	10
Aug. 2/64	Jan.26/65	177	2.95	1.91	35
Aug. 4/64	Feb.22/65	202	4.77	3.86	16
Aug. 12/64	Feb.22/65	194	1.59	1.36	14
Aug. 26/64	May 2/65	250	3.18	2.54	20

Plate I Gonad development in summer steelheads after leaving salt water. The three specimens were captured on August 13, 1965, and held in a fresh water pond until killed. 1. Gonad/body ratio 0.009, held 11 days; 2. Gonad/body ratio 0.020 held 69 days; 3. Gonad/body ratio 0.072 held 160 days.


3
2
1

in the summer and 8° - 10° C in the fall and winter. Fish were weighed, measured and tagged with a numbered Peterson disc tag at time of capture and re-weighed when killed. Weight changes in these specimens are summarized in Figure 16. It is apparent that a progressive decrease occurred in the weight of the individuals between August, 1965, and February, 1966. These data corroborate the observations made on fish from San Juan River tagged in 1964 and captured later in that stream. Plate I shows change in Gonad/body relationship with increased fresh water residence.

The course of events in maturation of both summer and winter fish with respect to growth in body size and gonad development will be summarized and discussed more fully in a later section.

Figure 16. Weight loss in summer steelhead trout during final maturation period in fresh water. Fish were captured in San Juan River, British Columbia in August, 1965. Each symbol represents a single specimen, killed at the hatchery where fish were held.

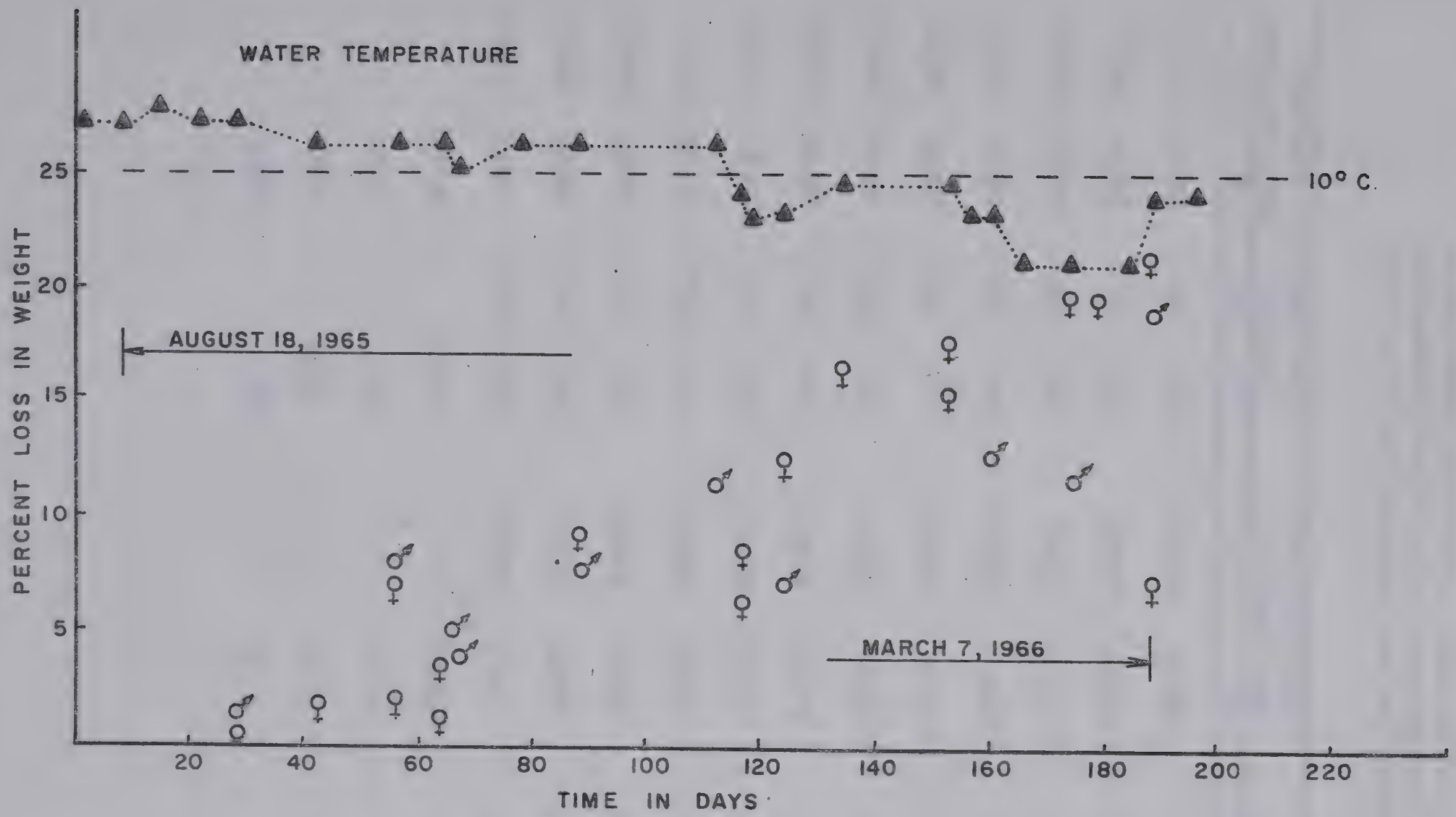

WATER TEMPERATURE
10° C.
AUGUST 18, 1965
MARCH 7, 1966
PERCENT LOSS IN WEIGHT
5
10
15
20
25
20
40
60
80
100
120
140
160
180
200
220
TIME IN DAYS

Table XIII Change in body weight in wild adult summer steelheads from San Juan River, British Columbia, held in a freshwater hatchery during final maturation of gonads.

Capture weight (gm)		Time held (days)		Weight when killed (gm)		Percent weight loss	
M	F	M	F	M	F	M	F
3570	1590	28	28	3535	1580	1.0	0.5
3740	3690	56	42	3710	3620	7.9	1.9
3970	2270	66	56	3810	2225	4.0	2.0
1700	3630	66	56	1615	3380	5.0	6.9
3290	5560	89	64	3230	5505	7.9	1.0
1590	4250	112	64	1410	4100	11.2	3.5
4710	2610	124	89	4360	2375	7.5	9.1
1930	1470	160	118	1695	1375	12.6	6.4
3180	5330	174	118	2805	4870	11.8	8.6
3290	4990	174	124	2805	4380	14.7	12.3
2840	2490	174	134	2280	2075	19.8	16.6
3520	2490	188	152	2855	2105	18.9	15.5
	1810		152		1490		17.7
	3000		181		2405		19.8
	3290		188		3035		7.7
	3690		188		2910		21.2

BODY FAT IN STEELHEAD TROUT

Body Fat in Experimental Populations

In adult steelheads which have recently migrated from the ocean into streams, large differences may be observed between summer and winter steelheads with respect to fat deposition in the body cavity. Summer steelheads have large depositions of fat around the stomach and intestine, while winter steelheads do not. Because these fish also exhibit marked differences in sexual maturation, examination of the levels of fat storage seemed warranted, both for adult and for juvenile fish of the two stocks. Young summer and winter steelheads were examined as yearlings and adults were examined after capture in spawning streams.

Several methods of estimating body fat in fishes may be used, including chemical extraction, histological examination of various tissues or measuring the occurrence of adipose depositions. The latter method was used in this investigation because of the ease of dissection and weighing a discrete fat body which lies on the dorsal surface of the stomach in S. gairdneri. The fat body in question is illustrated in Plate II, and is typical of all

S. gairdneri examined by the author. In antero-posterior extent, the fat body begins at the posterior end of the esophagus and extends approximately as far behind the posterior curvature of the stomach as it does in front. Ventrally, the adipose tissue descends no further than the ventral surface of the spleen, which is partially imbedded in it. Lying on the dorsal median surface of the stomach, the fat body rises dorsally as a sharp-edged keel, the base of which is approximately as wide laterally as one-half the lateral diameter of the stomach. The adipose tissue extends well over the anterior intestine, which loops posterior and dorsal from the pyloric sphincter, and is closely apposed to the dorsal intestinal surface, but not attached to it, except tenuously by weak and variable mesenteric connections. In some cases the fat body may be divided partially in the mid-dorsal region by a cleft, but complete separation of this tissue into two adipose bodies has not been observed in several hundred specimens examined.

For each specimen, the fat body was stripped from the stomach surface and weighed to the nearest mgm. Fat weight was plotted against body weight on arith-

Plate II Visceral fat on stomachs of yearling summer and winter steelhead trout. Top specimen is stomach of yearling winter steelhead weighing 39 gm; weight of fat on stomach is 19 mgm. Bottom specimen is stomach from yearling summer steelhead weighing 36 gm; weight of fat on stomach is 117 mgm. Fish were same age and both were females.

metic axes for each of the summer and winter stocks, combining all specimens and both sexes within each stock. Clear separation of the two stocks is apparent in these data, presented in Figure 17, but no correlation could be shown (Figure 18) between fat weight and gonad weight in yearling fish in either of the two stocks. Apparently differences in fat storage precede differences in gonad development by a considerable degree.

Body Fat in Wild Populations

Data are presented in Figure 19 to show the relationship between storage fat and gonad weight in adult summer and winter steelheads newly arrived in spawning streams from the ocean. Within samples of summer fish from Dean, San Juan and Capilano Rivers, no significant correlation could be shown between weight of visceral fat and weight of gonad. However, when samples from all three rivers are combined, the resulting plot shows an obvious inverse relationship between weight of visceral fat and gonad weight. Similar results are obtained for winter steelheads by plotting weight of visceral fat against gonad weight, although the inverse relation-

Figure 17. Relation of visceral fat weight and body weight in F_1 yearling summer and winter steelhead trout.

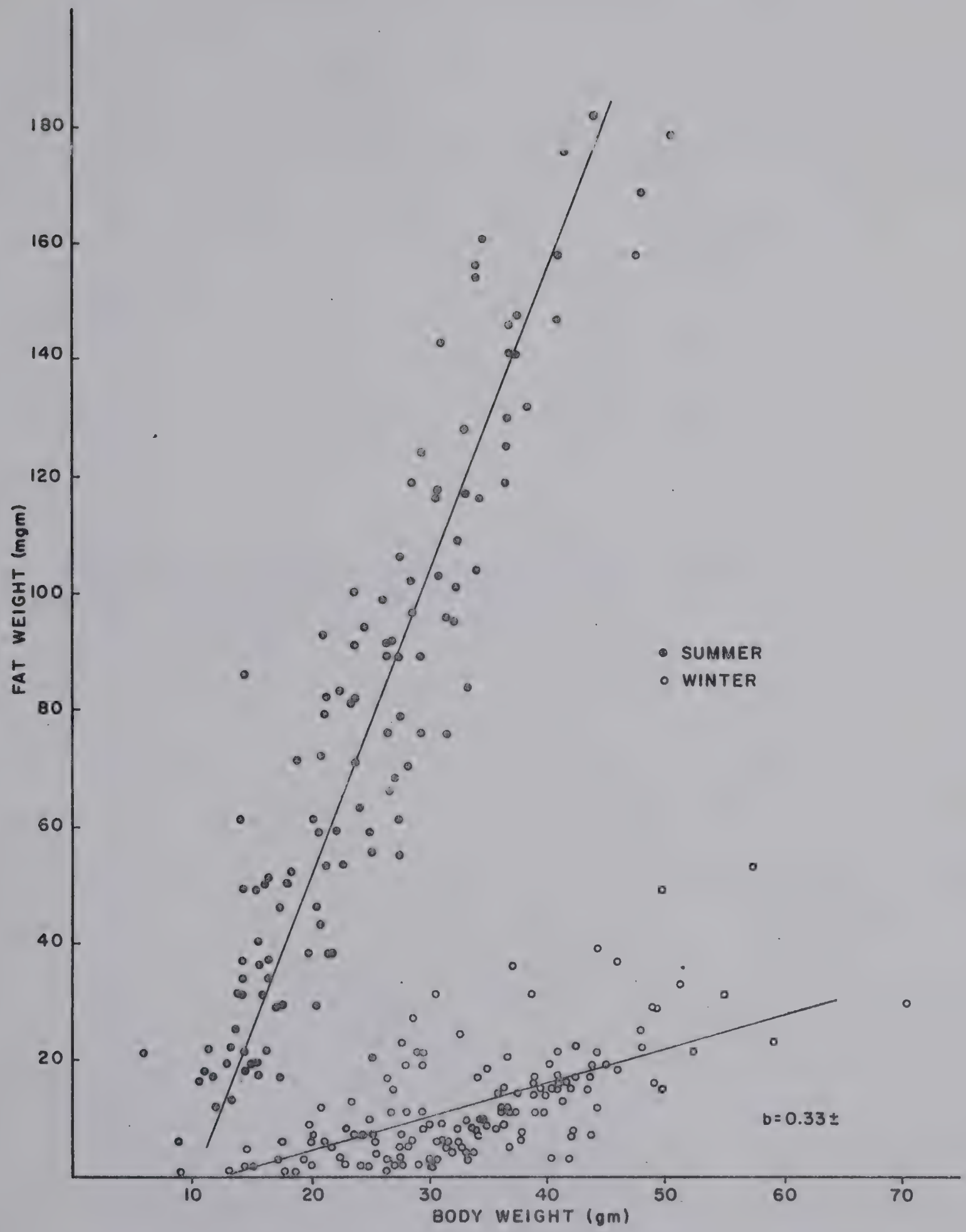

FAT WEIGHT (mgm)
180
160
140
120
100
80
60
40
20
10
20
30
40
50
60
70
BODY WEIGHT (gm)
SUMMER
WINTER
b=0.33±

Figure 18. Relation between visceral fat weight and gonad weight in F_1 yearling summer and winter steelhead trout.

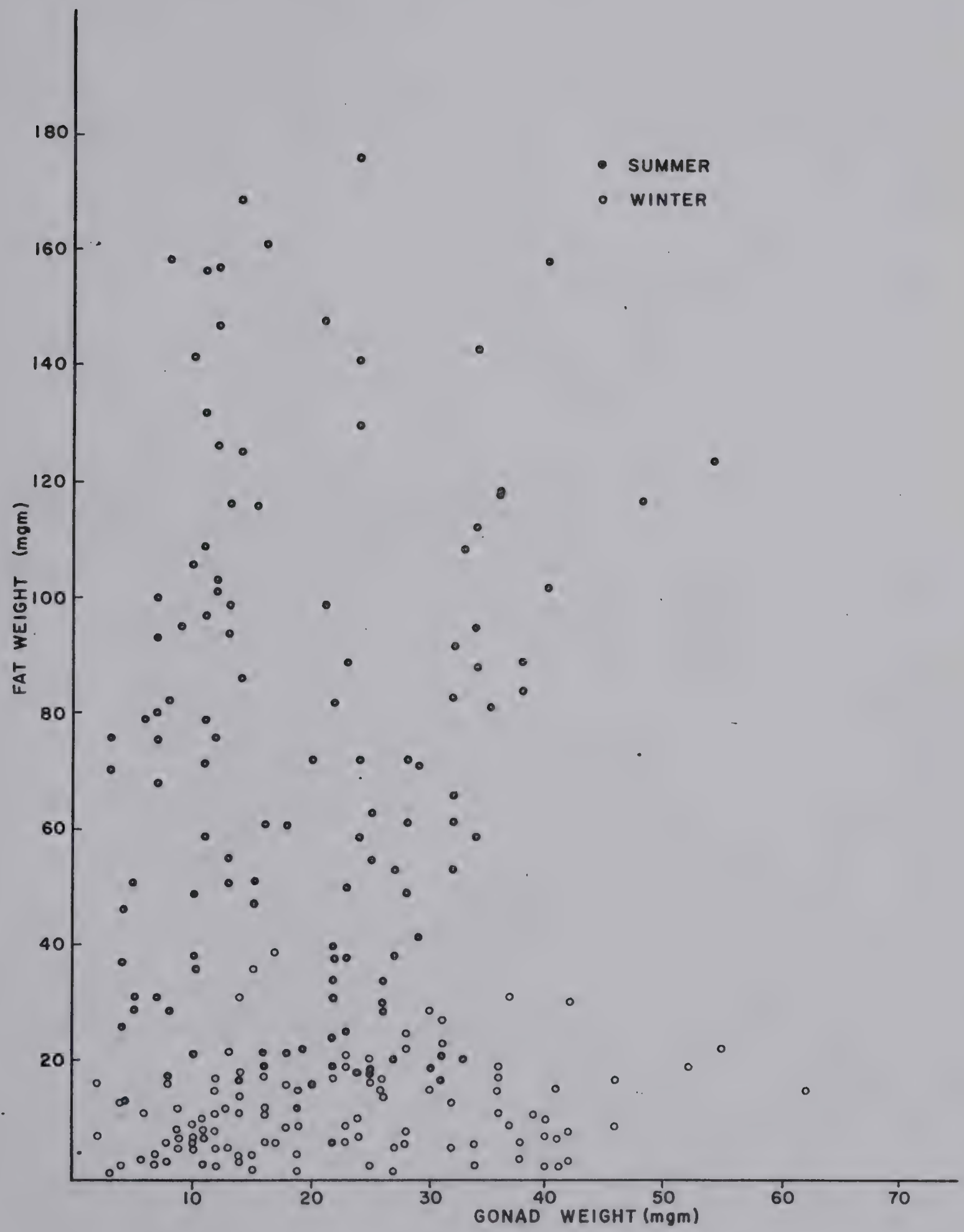
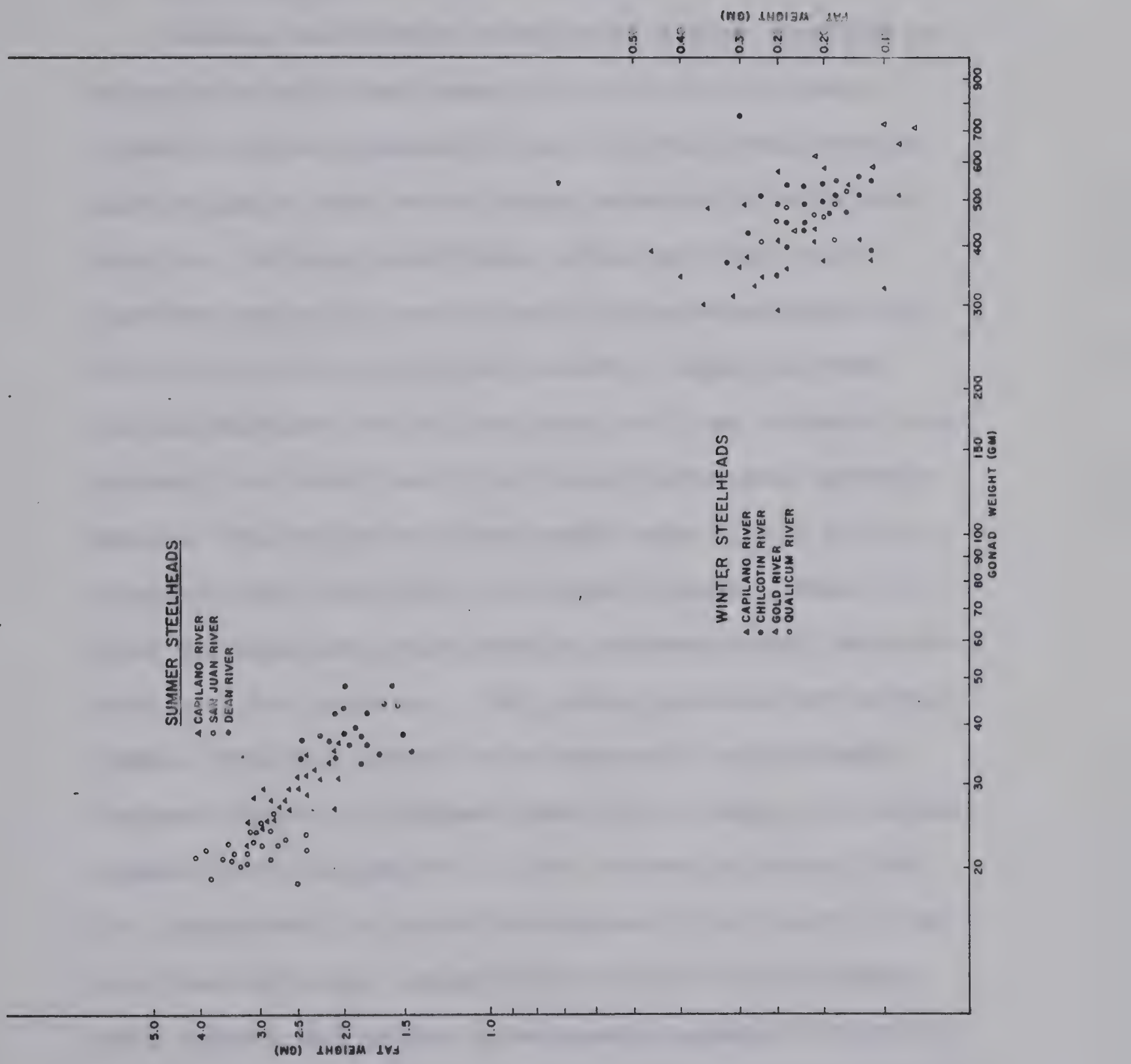

SUMMER
WINTER
FAT WEIGHT (mgm)
180
160
140
120
100
80
60
40
20
10
20
30
40
50
60
70
GONAD WEIGHT (mgm)

Figure 19. Relation between visceral fat weight and gonad weight in adult summer and winter steelhead trout at time of entry to spawning streams.


SUMMER STEELHEADS
▲ CAPILANO RIVER
○ SAN JUAN RIVER
● DEAM RIVER
WINTER STEELHEADS
▲ CAPILANO RIVER
● CHILCOTIN RIVER
△ GOLD RIVER
○ QUALICUM RIVER
FAT WEIGHT (GM)
GONAD WEIGHT (GM)

ship of visceral fat and gonad weight is less obvious in winter fish.

Summer and winter steelheads differ greatly in appearance and development on leaving the ocean. Summer fish are generally more silvery and females particularly show no evidence externally of mature ovaries. Winter steelheads often are dark and females typically are bulged in the antero-ventral region by fully developed gonads. Even the most casual examination of the body cavities reveals that summer fish have heavy fat depositions and immature gonads, while winter steelheads have little or no visceral fat and fully developed gonads. There is thus an apparent relationship between gonad development and fat storage. For young, pre-migrant steelheads, however, there is no apparent relationship between gonad development and fat storage. It would appear that the amount of fat stored by young fish is independent of gonad development, at least up to the time at which these fish migrate to the ocean. Both summer and winter steelheads generally migrate to the sea at a length of about 20 cm and a weight of approximately 45 gm.

Weight-length Relationships

When comparing body fat levels, it was necessary to eliminate the possibility that neither of the two experimental stocks of steelheads was in better condition than the other. Weight-length relationships in the two stocks were therefore compared by plotting weight against length on double logarithmic axes, both for yearlings in fresh water and for ages II and III in salt water. No obvious differences in the weight-length relationships could be demonstrated. The statements above can also be applied to wild, adult fish. Population samples of summer steelheads from Dean, San Juan and Capilano Rivers and of winter fish from Capilano, Gold, Chilcotin and Qualicum Rivers were compared on the same basis as for experimental fish. Again, no obvious differences were apparent in the weight-length relationships for these population samples.

Logarithmic plots of comparisons of weight-length relationships outlined above are shown in Figures 20 and 21. Three conclusions may be reached concerning condition of fish and the storage of fat in steelhead trout: (1) For experimental stocks of summer and winter steelheads reared for a year in fresh water under the

same environmental conditions and for the same stocks reared for two years under similarly uniform conditions in salt water, differences in body fat are not related to condition of fish. (2) The weight-length relationship appears to be remarkably uniform over an extended range in size in seven population samples of fish which had spent part of their life in the ocean. (3) Insofar as the amount of visceral storage fat may be representative of the total level of storage fat and not related to condition of fish, the differences in storage fat levels between summer and winter steelheads appear to be under genetically determined physiological control.

TEMPERATURE TOLERANCE IN YEARLING STEELHEADS

Range in resistance time for winter steelheads was 301 to 440 minutes and for summer steelheads from 286 to 386 minutes. Mean resistance times were compared by a "t" test. The means were significantly different ($P < 0.01$), indicating that summer steelhead yearlings were significantly less tolerant than winter yearlings to temperatures near the upper lethal limit. The differences in temperature tolerance probably are a reflection of differences in levels of storage fat in the two groups (Hoar and Cottle, 1952).

Figure 20. Weight-length relationships in fresh and in salt water, for F_1 summer and winter steelhead trout prior to maturation.

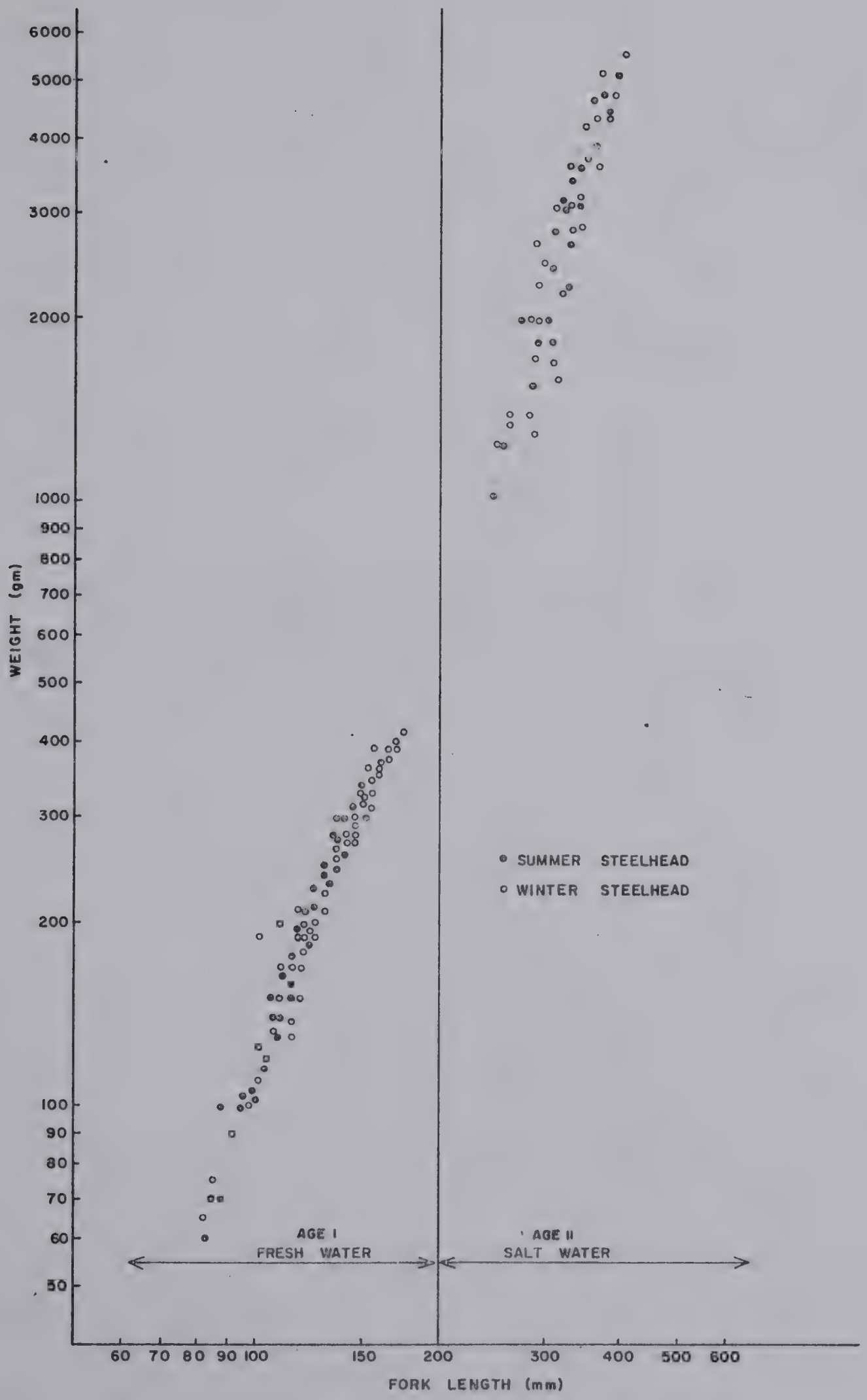
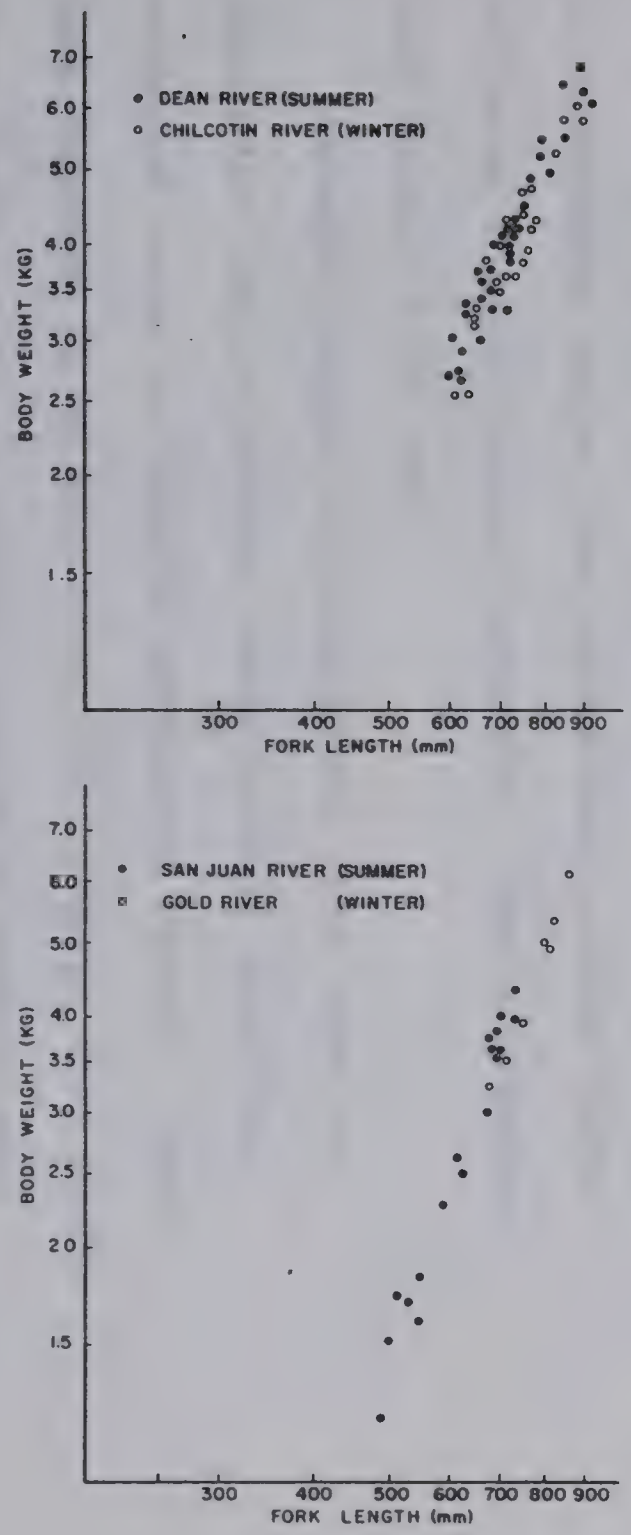
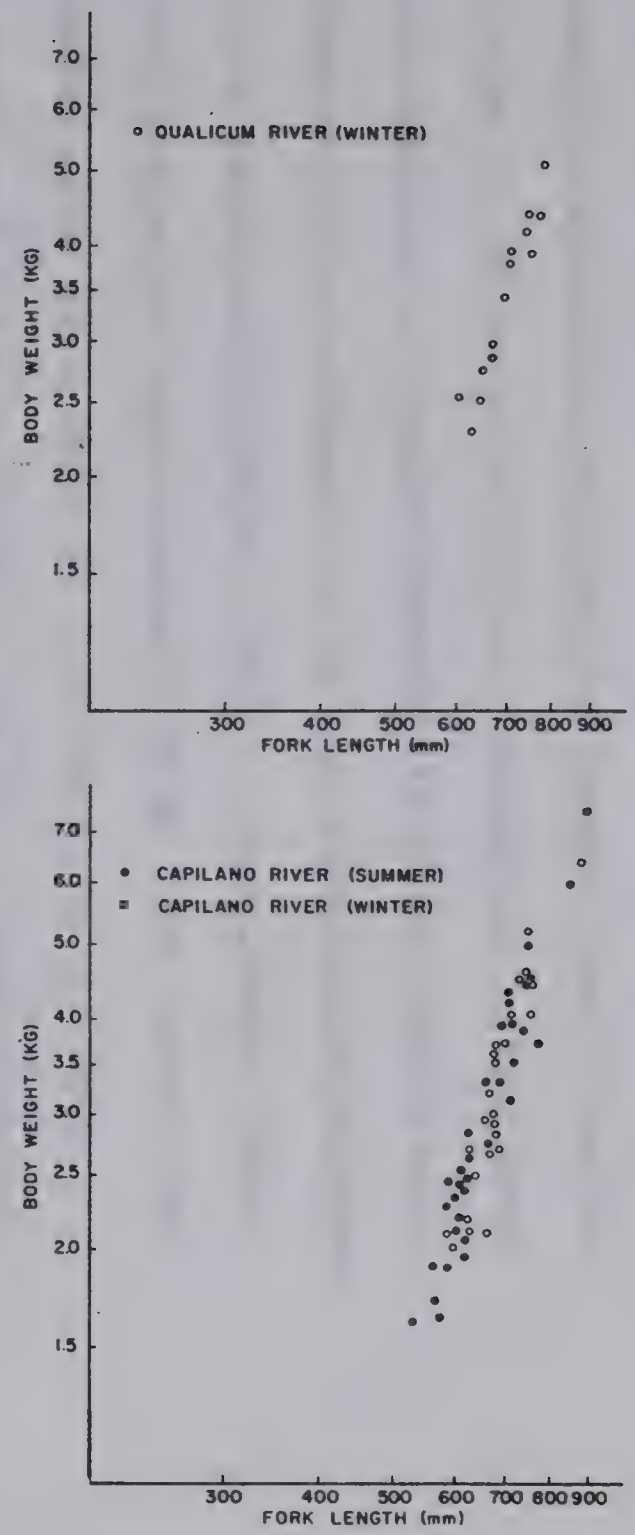

WEIGHT (gm)
6000
5000
4000
3000
2000
1000
900
800
700
600
500
400
300
200
100
90
80
70
60
50
SUMMER STEELHEAD
WINTER STEELHEAD
AGE I
FRESH WATER
AGE II
SALT WATER
60 70 80 90 100 150 200 300 400 500 600
FORK LENGTH (mm)

Figure 21. Weight-length relationships in adult summer and winter steelhead trout captured from British Columbia streams.


DEAN RIVER (SUMMER)
CHILCOTIN RIVER (WINTER)
BODY WEIGHT (KG)
7.0
6.0
5.0
4.0
3.5
3.0
2.5
2.0
1.5
300
400
500
600
700
800
900
FORK LENGTH (mm)


QUALICUM RIVER (WINTER)
BODY WEIGHT (KG)
7.0
6.0
5.0
4.0
3.5
3.0
2.5
2.0
1.5
300
400
500
600
700
800
900
FORK LENGTH (mm)

SAN JUAN RIVER (SUMMER)
GOLD RIVER (WINTER)
BODY WEIGHT (KG)
7.0
6.0
5.0
4.0
3.5
3.0
2.5
2.0
1.5
300
400
500
600
700
800
900
FORK LENGTH (mm)

CAPILANO RIVER (SUMMER)
CAPILANO RIVER (WINTER)
BODY WEIGHT (KG)
7.0
6.0
5.0
4.0
3.5
3.0
2.5
2.0
1.5
300
400
500
600
700
800
900
FORK LENGTH (mm)

(100)

GROWTH CALCULATIONS

Scale/length Relationship

Dorso-ventral diameters of scales were plotted against fork lengths of fish on double logarithmic axes for specimens ranging in length from 35 mm to 830 mm (1.38 in to 32.7 in). Essentially the same relationship in scale diameter to body length was observed in steelheads as in non-anadromous rainbow trout reported by Smith (1955). Steelheads first form scales at approximately 38 mm fork length and scales grow at a rate of 3.90 relative to body length until fish attain a length of approximately 50 mm. At 50 mm body length and a scale size of 25 micrometer units, the scale/body growth curve inflects sharply toward isometry. One micrometer unit equals 0.033 mm.

Several groups of steelheads were used to determine the scale/body relationship over the extended range in lengths mentioned above. Specimens between 35 mm and 70 mm fork length were drawn from Capilano River stocks reared at Summerland Trout Hatchery. Specimens between 70 mm and 180 mm were obtained from groups of yearling Capilano fish

reared experimentally at Cultus Lake Trout Hatchery and used for taxonomic and physiological comparisons of young fish. Capilano River stocks reared in salt water at the Pacific Biological Station, Nanaimo, British Columbia provided specimens in a saltwater environment in the size range 190 mm to 400 mm. Scale samples taken from specimens obtained in high seas catches in the Pacific Ocean by vessels of the Fisheries Research Board of Canada provided data for fish in the marine habitat in the length range 330 mm to 830 mm.

Calculations of Fish Lengths From Scales

The plots of scale size on body length are shown in Figure 22. The regression slopes for all plots, above a scale size of 25 micrometer units and a fork length of 50 mm do not differ significantly from a value of 1.00. ($P \geqslant 0.05$). Thus, above the inflection point in the scale/body relative growth curve, calculations of fish lengths from scale size can be made on the basis of direct proportion. However, allowance must be made for the initial size of the scale pocket at the time of scale formation and the rate of growth of the scale below the inflection point. All calcula-

Figure 22. Relationship between scale diameter and fork length in steelhead trout.

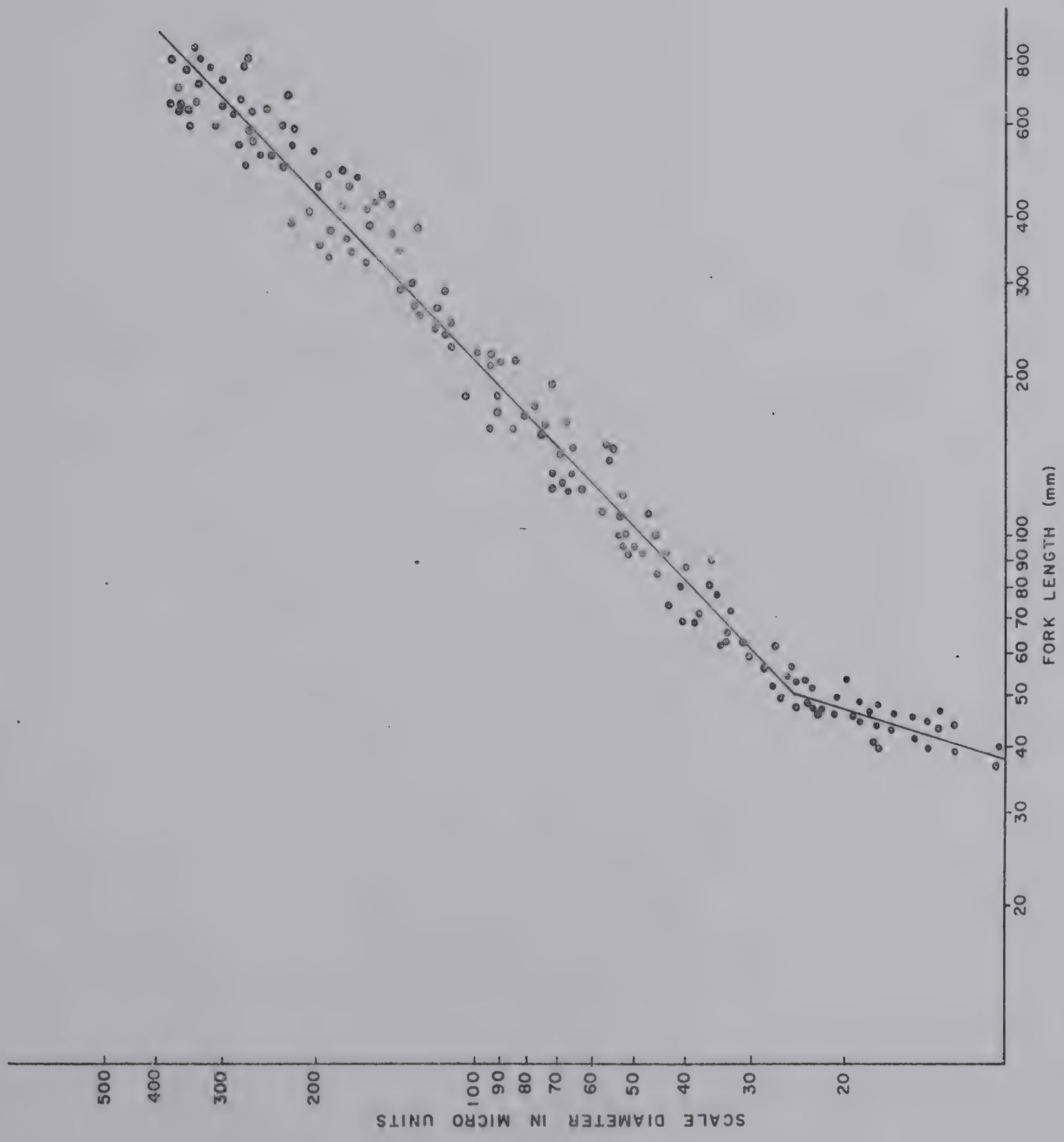
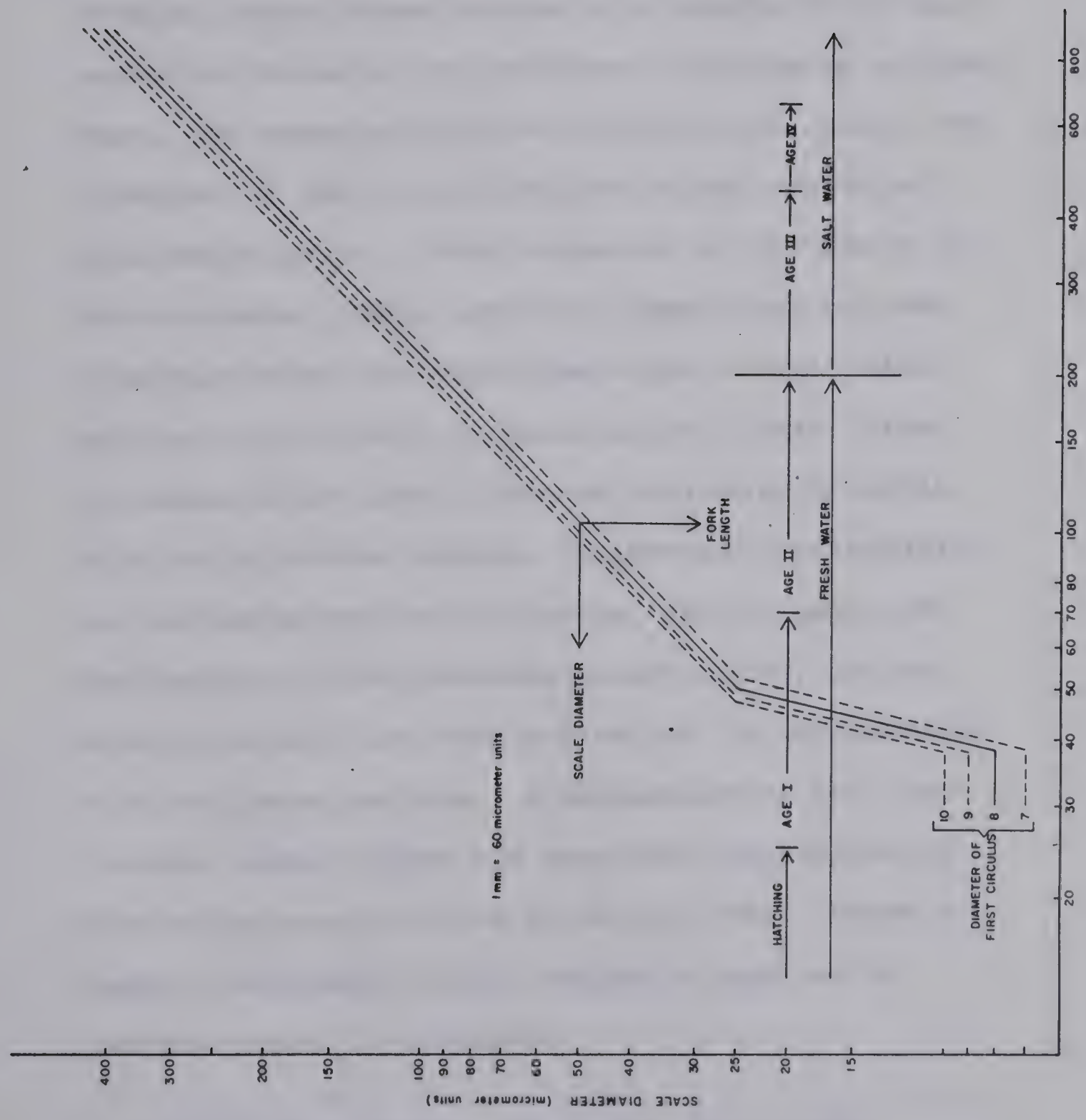

SCALE DIAMETER IN MICRO UNITS
500
400
300
200
100
90
80
70
60
50
40
30
20
FORK LENGTH (mm)
20
30
40
50
60
70
80
90
100
200
300
400
600
800

Figure 23. Method of calculating lengths from scales of steelhead trout (see text for explanation of method).


SCALE DIAMETER (micrometer units)
400
300
200
150
100
90
80
70
60
50
40
30
25
20
15
1 mm = 60 micrometer units
SCALE DIAMETER
FORK LENGTH
HATCHING
AGE I
AGE II
AGE III
AGE IV
FRESH WATER
SALT WATER
DIAMETER OF FIRST CIRCULUS
10
9
8
7
20
30
40
50
60
70
80
100
150
200
300
400
600
800
FORK LENGTH (mm)

tions of fish lengths to follow were based on a family of curves shown in Figure 23. A datum point was established for each specimen (assuming that all fish formed scales at a length of 38 mm.), using the diameter of the first circulus as a reference. An example is shown in Figure 23, where the diameter of the first circulus on the scale is 8 micrometer units. Total diameter of the scale is 50 micrometer units, and fish length may be read directly below the point where the 50 unit line on the "scale" axis intersects the 8 unit "first circulus datum line". Errors obviously occur in such calculations because of inherent variability in the scale/body relationship, in the point of inflection in the relative growth curve, in the size at which fish form scales, or in any combination of these factors. A discussion of the theoretical significance and practical advantages of the method may be found in Smith (1955), where a test of accuracy for the method as applied to rainbow trout is provided.

Growth of Wild Summer and Winter Steelheads

Growth calculations for adult wild steelheads from Capilano River were made both for summer and

winter stocks from scales used in a previous study on that stream (Withler, 1966). Calculated lengths of fish at the end of each year of life, both in fresh water and in the marine environment were used in comparisons of growth between the two stocks. Only the growth rates of fish of the same age and life history category were used in the comparisons. Thus, all fish compared went to sea at the same age and returned to fresh water at the same age. Fish which went to sea at age II and spent two years in salt water are categorized as 2/2. Categories 1/, 4/, /1 and /4 are represented by such small numbers of fish in Capilano River that these groups were not used for comparisons, which were restricted to 2/2 and 3/2 fish in both stocks. Table XIV summarizes growth data, both for fresh and for saltwater residence.

From Table XIV it is apparent that growth of fish in the same life history categories is very nearly the same for all groups in each stock. Two exceptions may be noted in that summer fish in the 2/2 category were significantly larger than winter fish in the same category ($P < .05$) at the completion of their second year in fresh water and at the end of

Table XIV Calculated lengths of summer and winter steelhead trout from Capilano River. (Numbers in brackets refer to sample size).

Stock and life history categories		Calculated lengths at various years (mm) fresh water 1/	2/	3/	salt water /1	/2
Summer steelhead 2/2	(23)	52	143	-	434	686
			NS	S	S	S
Winter steelhead 2/2	(19)	56	117	-	443	669
Summer steelhead 3/2	(28)	48	88	132	447	671
			NS	NS NS	NS	NS
Winter steelhead 3/2	(25)	55	82	130	457	676

↕ S Differences in means are significant ($P < 0.05$)

↕ NS Differences in means are not significant ($P > 0.05$)

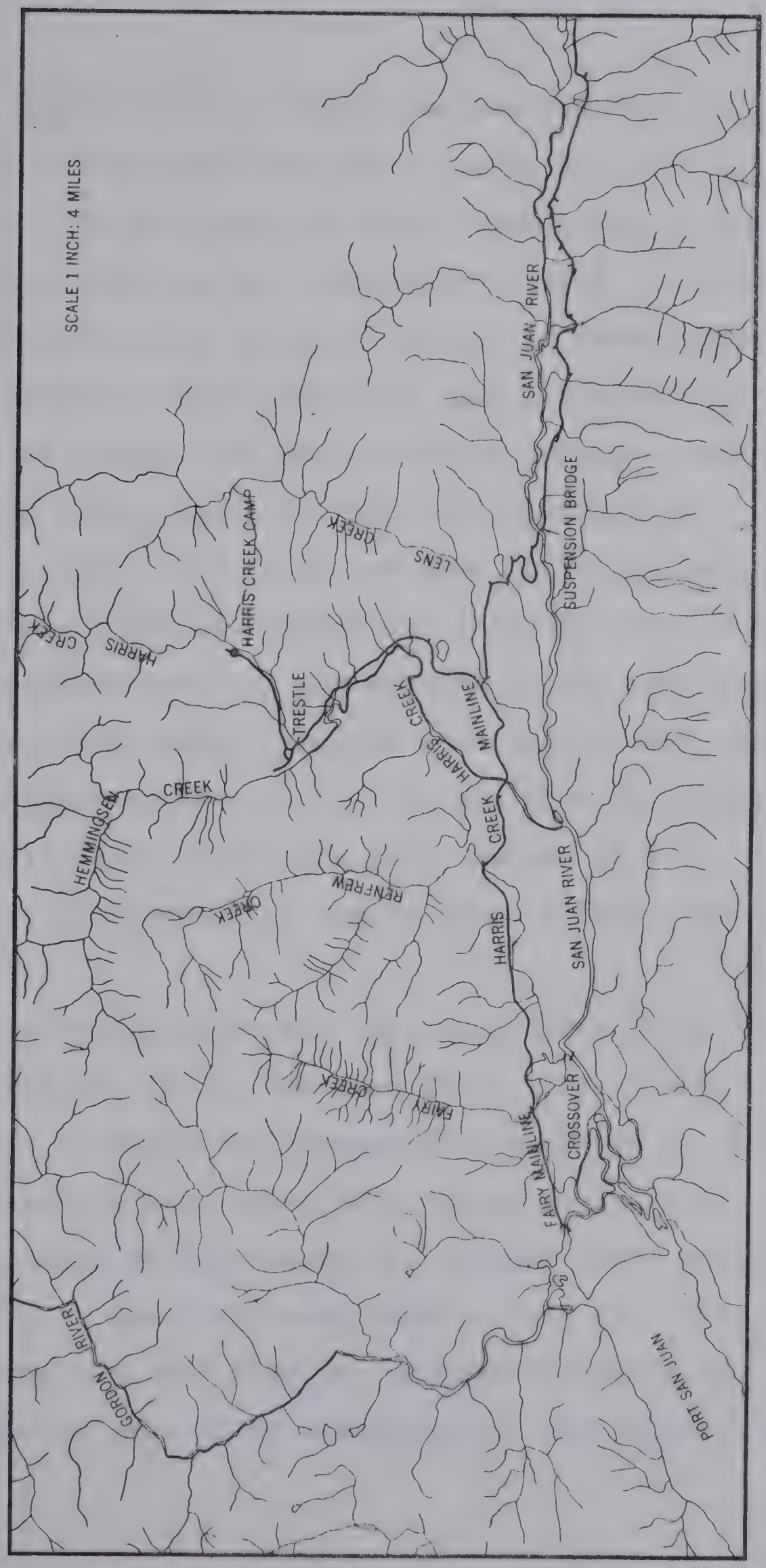
their second year in salt water. There is however, no clear evidence that differences in migratory behaviour and maturation patterns are associated with consistent differences in growth rates in the two stocks.

MIGRATORY BEHAVIOUR

Summer Steelheads in San Juan River

During the summer (June through August) in 1964, observations were made on the migratory behaviour of summer steelheads in San Juan River, Vancouver Island. San Juan River and its tributaries, together with important reference points concerned with this study, are shown in Figure 24. At a fish fence (Crossover) which blocked all adult fish migrating in the river, 112 steelheads were trapped, anesthetized with methyl pentanol, tagged and released to the river upstream of the fence. White and/or blue tags and baffles, 9/16" in diameter, of the Petersen disc-and-pin type, were fastened through the dorsal musculature, anterior to the dorsal fin of the fish. Neither tag loss nor tagging mortality was assessed, but no dead fish were observed in the river upstream of the fence, and all marked steelheads subsequently sighted by skin divers or captured by anglers bore tags with no evidence of injury to the fish. Prior to, during and following the tagging operations, Weksler temperature recorders were maintained on the

Figure 24. San Juan River, British Columbia, showing tributaries and reference points related to migratory behaviour of summer steelhead trout.


SCALE 1 INCH: 4 MILES
SAN JUAN RIVER
SUSPENSION BRIDGE
HARRIS CREEK CAMP
HARRIS CREEK
TRESTLE CREEK
MAINLINE
HARRIS CREEK
HEMMINGSEN CREEK
RENFREW CREEK
HARRIS CREEK
SAN JUAN RIVER
FAIRY CREEK
FAIRY MAINLINE
CROSSOVER
GORDON RIVER
PORT SAN JUAN

two major tributaries comprising the San Juan River system (Harris Creek and the mainstem San Juan River). The total run of summer steelheads in the San Juan River was not trapped and tagged. Visual observations, plus anglers' catches of steelheads above the fish fence indicated that a substantial number of summer fish had proceeded upstream past the trap site before the fence was operable on July 23, 1964. The fence had been installed earlier (on July 14) but had washed out in heavy rains which were characteristic of the weather in the area during the preceding month. Anglers reported heavier than usual concentrations of fish in the upstream pools on Harris Creek during the early summer of 1964, probably as a result of the relatively high river flows.

During and after the tagging program (July 25 to August 29, 1964), San Juan River in part and portions of tributary streams were examined by the author and others, using skin diving gear. First observations by the author and another diver while swimming in the river were made on July 29, 1964. The river was swum from the Suspension Bridge for a distance of 10.5 miles downstream to the fence at the

Crossover (Figure 24). All crevices in rocks, ledges under cliffs, deep holes (to a depth of approximately 20 feet) and spaces under logs or roots were examined diligently in search of steelheads. No adult steelheads were observed from the Suspension Bridge to the mouth of Harris Creek. Several hundred coho salmon yearlings and fish of the year (Oncorhynchus kisutch), a few rainbow trout (possibly pre-migrant steelheads, Salmo gairdneri) and a few cutthroat trout (S. clarki) were seen in the reach of the river examined. These fish often could be approached within a few feet. Lateral visibility in the river was very high (over 50 feet) and it is highly improbable that adult fish of any species could have gone unnoticed. Flow in the mainstem San Juan River was approximately 200 cfs on July 26, 1964. Between the mouth of Harris Creek and the Crossover at the fence site, 39 tagged steelheads were observed on July 29, 1964.

On the six days prior to these observations, 73 summer steelheads had been tagged at the fence and released upstream. San Juan River was again swum by the author from the Suspension Bridge to the mouth of Harris Creek on September 4, 1964. No tagged or untagged summer steelheads were seen, although 16 adult

coho salmon were observed, plus 9 other large salmonids which appeared to be cohos, but which could not be identified positively. Spot checks with diving gear were made on San Juan River upstream as far as 9 miles above the Suspension Bridge, between August 26 and September 30, 1964. No tagged steelheads were observed during these spot checks, but several hundred cohos were positively identified at close range under water.

Harris Creek twice was swum from Old Harris Creek Camp to its confluence with San Juan River (on September 16 and on October 2, 1964). Some parts of Harris Creek could not be covered because of waterfalls or stretches of water with rapids, but all pools and channels with suitable depths or velocities were carefully examined. In all pools with slack water near the bottom, steelheads were observed on or near the bottom of the stream. Of 29 steelheads positively identified during these swimming observations, 11 were tagged with Petersen disc tags of the same color as those applied at the fence site. As in San Juan River, lateral visibility in Harris Creek was extremely high (at least 50 feet). In most parts of Harris

Creek, the bank on either side could be seen clearly from the center of the stream while the observer was under water.

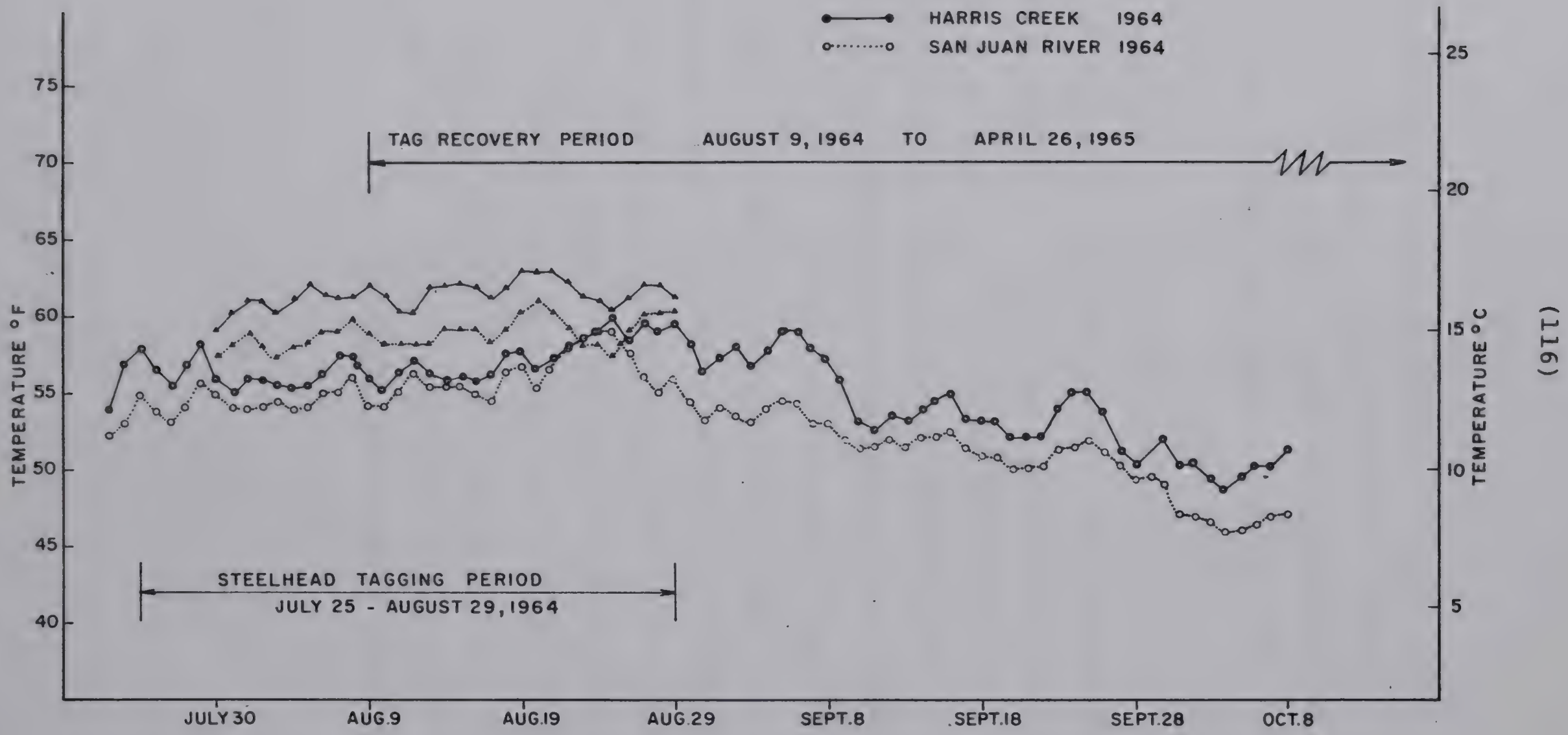
Two pools were examined from the bank of Hemmingson Creek, about one-half mile above its confluence with Harris Creek. Three steelheads were seen, one of which was tagged with white Petersen tag with blue baffle, a color combination used at the fence on August 12, 1964.

During the tagging program, the first tagged steelhead was caught by an angler in 12-Mile pool on Harris Creek. The fish was tagged on July 28 and the tag was returned on August 9, the day of capture. Between the date of first and last tag return (August 9, 1964 and May 2, 1965) no tagged fish were reported taken in San Juan River either below the fence site or above the mouth of Harris Creek, except for 3 spent fish which were taken near the Suspension Bridge. These fish had spawned several weeks previous to their capture, were in good condition and were silvery in appearance. No tagged or untagged fresh summer steelhead has ever been reported to the author from San Juan River above the confluence

of the river with Harris Creek. Interviews with 27 anglers on San Juan River resulted in unanimity of agreement that summer steelheads are not taken in San Juan River above the mouth of Harris Creek during summer months.

It is apparent from the foregoing that summer steelheads on the San Juan system exhibit an extremely strong (and perhaps total) preference for the Harris Creek portion of the San Juan River drainage, or that some factor exists in the character of mainstem San Juan River which excludes them from that portion of the drainage system.

Temperature records, tagging dates and recovery dates on the system are summarized in Figure 25. No apparent correlation exists between river flows and temperatures and entry of fish to the trap. During the period of observation on migratory movement of summer steelheads, temperatures were consistently higher in Harris Creek than they were in the mainstem San Juan River.


HARRIS CREEK 1965
SAN JUAN RIVER 1965
HARRIS CREEK 1964
SAN JUAN RIVER 1964
TAG RECOVERY PERIOD AUGUST 9, 1964 TO APRIL 26, 1965
STEELHEAD TAGGING PERIOD
JULY 25 - AUGUST 29, 1964
TEMPERATURE °F
75
70
65
60
55
50
45
40
TEMPERATURE °C
25
20
15
10
5
JULY 30
AUG. 9
AUG. 19
AUG. 29
SEPT. 8
SEPT. 18
SEPT. 28
OCT. 8

(116)

Figure 25. Temperature, tagging dates and recovery dates of tagged summer steelhead trout on San Juan River and Harris Creek, British Columbia, 1964 and 1965.

Winter Steelheads in San Juan River

Direct observation of steelheads in San Juan River during winter months is difficult because of high water flows. However, angler checks by Conservation Officers of the British Columbia Fish and Wildlife Branch provide some information on migratory behaviour of winter fish in the system. Scale samples obtained from angler-caught winter fish indicate that few winter steelheads ascend the San Juan system before December, and that fresh, unspawned fish may be taken as late as the first week in May. The pattern of migration which may be deduced from angler catches of winter steelheads in this river is little different from that observed in many other British Columbia streams and in streams of Pacific drainages of Washington, Oregon and California (Pautzke and Meigs, 1940; Withler, 1966; Shapovalov and Taft, 1954.)

Summer Steelheads in Other Streams

In Coquihalla and Silver Rivers, near Hope, British Columbia, summer steelheads were observed as early as May 21, 1956, although large numbers of summer fish were not observed in those two streams

until late June of that year (G. Dibblee, unpub. rpt., B.C. Fish and Wildlife Branch).

In Capilano and Seymour Rivers near Vancouver, British Columbia, summer steelheads generally appear by early May. In Capilano River in 1959, summer steelheads were captured in fish traps three miles above tidewater in late April.

In Dean River, approximately 300 miles north of Vancouver, summer steelheads are present in substantial numbers from the end of July until early September. In Gordon River, near Port Renfrew, Sarita River, near Bamfield, Heber River, near Tahsis (all on Vancouver Island) and in Brem River, near Ocean Falls, British Columbia, summer steelheads have been observed in July and August, by the author.

Although precise information on speed of migration is not available for summer fish in any river, specimens were seen over two miles upstream of an obstruction in Coquihalla River on the day following first successful passage of a falls. On the day previous, no fish had been observed in the upper river above the falls, although water was clear and visibility was good. Summer steelheads on Dean River have been reported to ascend that stream a distance of ten

miles after first passage of difficult water in the lower river on the previous day (R. Stewart, per. comm.).

Because of the relatively small size of many known populations of summer steelheads, it is assumed that populations of these fish in lesser-known streams are probably small also. D. R. Hurn (per. comm.) has confirmed the presence of summer steelheads in 24 streams on Vancouver Island and has reported, but not confirmed their presence in 7 other streams in the same area. A. Elsey and H. J. Rayner (pers. comm.) both have reported summer steelheads to occur in many streams between Vancouver and Prince Rupert, both on the mainland coast and on the larger islands along the coast of British Columbia. Reports of summer steelheads in streams along the coast of Alaska have not been documented by the author, although A. McRae (pers. comm.) has reported large rainbow trout in Alaska coastal streams in July and August. Reports on summer steelhead in streams on the Washington, Oregon and California coasts are infrequent in the literature on anadromous Salmo gairdneri, and no published account is available of the total distribution of summer steelhead south of

the Canada-United States border. It would appear that the total number of streams containing natural populations of summer fish is less than 10 in the southern Pacific coast states of the United States, while the approach to the northern limit of the range of S. gairdneri in Alaska probably limits the distribution of summer and winter steelheads alike in northern areas. The available evidence indicates that summer steelheads are to be found most commonly in British Columbia streams, and that a large proportion of the total number of populations in British Columbia exist in Vancouver Island streams.

Winter Steelheads in Other Streams

Most rivers in British Columbia contain winter steelheads, where access from the ocean for these fish is unimpeded. In some cases (e.g., Kispiox River) these fish may enter the streams as early as September, but generally, in most drainages, winter fish are not taken by anglers until October or November. Peaks of migration apparently occur in January through March on southern British Columbia streams (Withler, 1966) and somewhat earlier on northern streams (Lyons, pers. comm.). In Alaska, winter

steelheads are present from October to April, with January runs predominating (McRae, pers. comm.).

Commercial catches of steelheads provide some information on migration times for winter fish in Skeena and Fraser Rivers (Dept. Fisheries Canada Ann. Rpts.). Large seine and gillnet salmon fisheries operate off the mouths of these two rivers in late summer and early autumn, when steelheads are caught in substantial numbers. From the few samples examined by the author from commercial catches, it would appear that very few summer steelheads are taken in these two commercial fisheries. It is apparent that during the summer and early autumn salmon fisheries, steelheads are caught in increasing numbers from July through September. Since, as mentioned above, these are largely winter fish, it would seem that summer fish may approach the mouths of the larger rivers in the spring months, and that winter steelheads may commence their migration in late summer or early autumn, although the respective stocks generally are not seen or taken by anglers in streams in significant numbers until some time later. In Chilcotin River, in central British Columbia, winter steelheads are present from November through

April. It is not known whether there are distinct "early" or "late" runs of fish to this stream, as reported by anglers. In some years, pack and anchor ice is so prevalent in Chilcotin River that fish cannot migrate in that stream from early December to late April. Other, unknown environmental conditions in all streams make it difficult to assess catch statistics as a means of determining migratory times for winter fish.

Summary of Migratory Behaviour

Without extensive trapping facilities near the mouths of streams, it is not possible to record precisely the times of migration of steelheads from salt water, either for winter or summer fish. Nevertheless, Withler (1966) was able to determine approximate times of runs of steelheads from scale samples submitted by anglers from British Columbia streams. In general, it would appear that summer steelheads migrate toward the mouths of streams in late winter, early spring and summer, but they seldom are observed migrating in rivers before May or after September and predominantly in June through August. Winter fish appear to be present in salt

water near the mouths of at least the Skeena and Fraser Rivers from September to April, but predominate in streams from January through March. Where extensive data are available, it would appear that each stream is characterized by the presence of steelheads at a particular time of year, although as mentioned earlier, it is probable that for many streams, adult steelheads may be present in most months. Trapping records on San Juan and Qualicum Rivers and observations of migration on Coquihalla and Chilcotin Rivers indicate that stream environmental conditions play an important role in determining active migration upstream. Factors which may be important in determining the presence of either summer or winter fish in particular streams will be discussed later.

DISCUSSION

Descriptions of races or stocks of fishes of necessity may be restricted to use of characteristics which may be sharply affected by environmental influences. For instance, regulation and commercial exploitation of Pacific salmon is based largely on knowledge of the timing of spawning runs and size of populations produced from various freshwater rearing areas.

Timing of migration of sockeye salmon to different river systems can be important for reproductive success (Royal, 1961), since each stock of fish which utilizes a separate stream system appears to be adapted to a specific thermal regime for successful egg deposition and larval development. It is likely that isolated populations of Pacific salmon are composed of similar genotypes, because the timing of their migratory behaviour is predictable within fairly narrow limits for separate stream systems. With respect to these stocks, the application of criteria commonly used by taxonomists to separate populations of fishes might largely fail to indicate important differences in physiological

attributes (thermal requirements for successful spawning and larval development) or in behaviour (timing of migration). It is probable (Ricker, 1959) that as yet unrecognized genetic differences can and do exist in most, if not all stocks of Pacific salmon and steelhead trout. Ricker further suggests that there is probably little straying between populations under natural conditions, and that reproductive isolation is maintained through the mechanism of homing behaviour, although there is no physical barrier to prevent exchange in most stocks. Stocks of these fishes are therefore described and managed on the basis of their reactions to ecological conditions at various stages of their life histories, while taxonomic characteristics of the populations may be largely unknown.

It is often not convenient to study seasonal races or stocks because of disparity in spawning times and migratory behaviour. To the present little attempt has been made to sort out the factors which may be important in the separation of populations which may be mutually viable, but which do not interbreed. Detailed investigation of maturation processes affords the opportunity to explain racial

differences between stocks only when adult fish can be brought together in the same state of sexual maturity. Summer steelhead trout may live in nature for ten months without consuming significant quantities of food while maturing, and have been held for more than twelve months without food in a hatchery prior to spawning (Smith, 1960). Thus, these animals provide an unique opportunity to investigate reproductive processes over an extended period of time. Further, the young of steelhead trout are relatively easy to raise artificially, and conveniently can be followed into the F_2 or later generations because their life span is generally not more than four years. Races ("morphae") as described by Berg (1934), Rounsefell (1958), Smith (1960) and Zarnecki (1963) suggest that with respect to differential rate of gonad development and migratory behaviour, such physiological adaptations probably are widespread in anadromous salmonids. In addition, studies on Salmo salar and S. trutta by Zarnecki mentioned above, indicate that migratory behaviour of those two species in adult fish which have left the ocean is strikingly similar to the behaviour of seasonal races of steelhead trout. How-

ever, the literature appears to be devoid of reference to detailed examination of maturation in nature or to experimental evidence concerning the degree of genetic interchange between or control within populations. Further, little information is available on maturation characteristics as related to ecological conditions.

In the present study, very wide differences have been demonstrated in maturation of summer and winter stocks of steelhead trout reared under the same environmental conditions in salt water. Further, the young, pre-migrant individuals of the two stocks show essentially complete separation on the basis of the amount of visceral fat accumulated in the body cavity before migration to salt water. To a degree, these physiological differences are reflected in taxonomic differences (numbers of vertebrae, gill rakers and parr marks in experimental yearling fish and in numbers of vertebrae and gill rakers in wild, adult fish). Some caution should be used when interpreting results of statistical comparisons of meristic series, because the range in all characteristics overlap in most groups observed in this study. Variability in characteristics of progeny obtained from single sets of parents is such that small, but persistent differ-

ences between stocks may be masked unless large samples are available for comparisons. Thus, it was possible to show significant differences between groups of progeny in summer and winter stocks only when large numbers of fish were compared. For wild populations, differences between rivers within both summer and winter stocks could not be demonstrated, although significant differences between stocks could be shown if all samples from the summer fish were combined and compared with combined samples from the winter fish. These comparisons therefore suggest that summer and winter stocks are comprised of populations wherein the individuals are morphologically very similar, but where it is likely that interbreeding between stocks seldom occurs, because if these fish interbred to any significant degree, it is unlikely that significant differences in meristic characters could be detected.

Hoar (1963) has suggested that it is not necessary to postulate a specific endocrine system to account for migratory behaviour in salmonids and Northcote (1962) has shown that environmental influence (largely temperature) controls the migratory behaviour of young, non-anadromous Salmo

gairdneri in streams tributary to lakes. However, differences in maturation physiology of summer and winter steelheads are reflected in differences in migratory behaviour, particularly with respect to time of entry to fresh water spawning streams from the ocean. A similar connection has been shown by Zarnecki (1963) for S. salar and S. trutta populations of the Vistula River in Poland.

The maturation process in summer steelheads in salt water appears to be quiescent, or at the least, gonads of ocean fish are so slightly developed that clear separation of summer from winter stocks in salt water can be made on the basis of gonad development alone. Summer fish which are in a physical state not generally associated with sexual maturation (fatness, silvery colour, lack of significant quantities of reproductive tissue) nevertheless migrate to and take up residence in spawning streams in response to stimuli which, while not known, must be greatly different in degree, if not in kind to those to which winter fish respond. Summer steelheads enter rivers in which temperatures are rising, or in which they are at or near maximum levels, while stream flows are at the same time

dropping to summer minimums. Summer steelheads either enter streams or migrate toward their mouths when photoperiod is long, with migration rates maximized in a period approximately seven weeks on either side of the longest day in the month of June. Thus the direction of photoperiod increments is opposite for approximately equal time periods during stream entry from the ocean for summer fish, and does not appear to be significant in migratory behaviour of this stock.

Winter steelheads, on the other hand, migrate from the ocean in a state approaching sexual maturity (lack of body fat, often in spawning livery, advanced state of gonad development) and seldom are found in spawning streams before October, and with highest numbers in January through March (Withler, 1966). Water levels are very often rising, particularly in shorter coastal rivers and generally temperatures are dropping or are at or near winter minimums. Photoperiod is decreasing during the early part of the winter run and rates of migration for most winter populations are heaviest when day length is short, but increasing during the period January through March. In Capilano River (Smith, 1960) late

winter and early summer migrants may enter the stream from the ocean at the same time (late in April or early in May).

The migratory pathways and distances travelled by steelheads in the ocean is not known in detail but the locations of catches of these fish by high seas vessels, and the size attained by individual fish during ocean residence is available for several hundred specimens. These data suggest that steelhead trout attain their maximum size far from the influence of olfactory or other cues from freshwater streams which could act as stimuli to migration. Maher and Larkin (1955) and Withler (1966) both state that there is a lack of evidence to indicate a connection between migration times and size or age of fish. It is difficult to assess possibilities of stimuli to migration which fit all observed situations, yet timing of runs to many rivers is relatively uniform for each stock of fish. From the foregoing, it is suggested that summer and winter steelheads migrate toward spawning streams in response to an innate tendency to seek fresh water which acts at quite different times in the respective life histories of the members of the two stocks and during

stages of greatly different sexual development. It would thus appear that for various river systems stocks of steelhead trout have evolved in response to selective factors in the environment, and that each of these stocks migrates toward a particular stream in response to as yet unknown stimuli. In any event, migration and state of sexual development appear to be strongly associated. Migratory behaviour of adult steelheads could be regulated in part by different salinity preferences, in summer and winter stocks at certain stages in sexual development, and this could account for some of the observed differences in behaviour already noted.

Selective factors in the environment can best be understood after direct observation of physical response of steelhead trout to environmental conditions. Evidence was presented to indicate the extent of physical barriers to migration in Harris Creek, tributary to San Juan River, and in Coquihalla River. Winter steelheads occur in both these streams, but have not been observed in upriver areas where summer fish ascend waterfalls with greater than 11 feet vertical drop

(Coquihalla River) and 9 feet drop on Harris Creek. Not only are summer fish able to ascend these extremes, but also pass a series of cataracts over one mile in length before the waterfalls on both streams and pass through turbulent areas with high water velocities for a considerable distance past the obstructions. On Dean River, extremely turbulent water with high velocities occurs near the mouth of this stream a short distance above tidewater and for over ten miles in a series of canyons about twenty miles upriver. On Silver Creek, near Hope, British Columbia, and on Capilano and Seymour Rivers, near Vancouver, British Columbia, turbulent water occurs over long stretches of stream. All these streams contain populations of summer steelheads. In all streams in British Columbia where summer steelheads are known to occur, deep pools are characteristic and steelheads have been observed in these pools during summer months. In British Columbia, summer runs of steelheads have not been observed in any stream where deep pools and/or water velocities difficult to the passage of fish do not exist.

Results of selection have been observed in a number of fish populations, particularly with respect to time of maturation in trout and salmon. Whether selection is unintentional, as for instance in the harvest of natural populations, or by design, as practiced in fish culture, population characteristics can be altered rapidly (Smith, 1961). It is commonly recognized by fish culturists that time of maturation in trout can be advanced or retarded in fish populations in hatcheries by retaining only those fish which mature at the desired time and discarding those which do not. Thus by artificially maintaining gene flow in one direction, hatchery stocks of fish can be established which mature within close limits of any desired date. Such selection is less random and more rapid than that which can occur in nature and can accomplish the desired result in a comparatively short time. Brood stock populations of Salmo gairdneri now exist in North America in a large number of fish hatcheries in the United States in which fish mature in spring, summer, autumn and winter as desired for fish culture purposes. There is therefore ample evidence that S. gairdneri exhibits enough varia-

bility in its reproductive physiology to respond to selective pressure over a very wide range. Natural selection rates may be quantified theoretically, but in practice fish populations are seldom observed over a sufficiently long time to draw any but the broadest inferences concerning changes in population characteristics through selection.

In non-anadromous rainbow trout, lake-dwelling populations may successfully reproduce either in inlet or outlet streams, but the available evidence is against the existence of genetically distinct stocks in relatively small (<10 square miles) bodies of water (Northcote, 1962). Lindsey et al (1959) suggest that in the same body of water as that studied by Northcote, significant numbers of fish stray between inlet and outlet streams and that there is sufficient genetic interchange to preclude the possibility of establishing genetically different stocks. On the other hand, in Kootenay Lake in southern British Columbia, with an area greater than 150 square miles, Vernon (1957) demonstrated the existence of genetically different stocks of kokanee salmon, Oncorhynchus nerka, in at least three areas of the lake. Recent evidence

concerning rainbow trout from Kootenay Lake (Smith and Stringer, unpublished data) strongly indicates the existence of a population of fish in that lake, the individuals of which have a maturation physiology markedly different from that observed in any other population of the same species reported to the present time, either in Kootenay Lake or any other lake, and that the differences probably are genetically controlled. In the lake systems discussed above, there are no known physical barriers to free interchange between stocks. In the case of summer and winter stocks of steelhead trout, there may be physical barriers in streams which prevent the ascent by winter fish of steep stream gradients, but in some rivers the whole stream system may be utilized by both stocks. In all streams studied to date, winter steelheads have been recorded in the same streams where summer fish are known to occur, but in the majority of Pacific coast streams, winter fish only are present. Thus, the occurrence of summer fish cannot be related only to stream conditions.

During migration of adult summer steelheads, stream temperatures may exceed 17° C (63° F). Thus summer fish are exposed to thermal conditions

greatly different than those which occur when adult winter fish are resident in streams, when winter stream temperatures approximate 5-6° C. It would appear that metabolic rates of adult summer steelheads in streams should be at least double those of winter fish, on the basis of the Q_{10} approximation. Yet summer fish which spend up to ten months in stream (often for two to four months at relatively high temperatures) exhibit a post-spawning mortality not greatly different from that of winter fish (Withler, 1966). Stream temperatures where summer fish have been recorded may remain relatively high ($>14^{\circ}$ C) from June to September (San Juan River), or may seldom approach that level (Capilano River, Seymour River). In some cases (e.g., San Juan River in 1965) low flows and high temperatures may persist from May to October. In San Juan River in August, 1965 there was no evidence of stratification or cold water intrusions in deep pools measured at a depth of more than 11 m (34 ft), and stream temperatures exceeded 17° C. Summer fish may therefore be exposed for long periods of time to thermal conditions which appear to be extreme for a poikilothermic animal meeting the simultaneous

demands of metabolic functions and final maturation of gonads.

Stream resident adult steelheads generally do not consume significant quantities of food. For winter fish, recently arrived from the ocean and exposed for a relatively short time to water temperatures of 2-5^{o} C before spawning, a smaller demand is made on energy stores than for summer fish. It would appear that the lipid reserves of summer fish may not be sufficient to satisfy metabolic demands and the requirements for building reproductive tissues. Atresia rates in ovaries of summer steelheads are so high as to suggest that metabolic requirements may be partially met by withdrawal of material from these organs. Although not observed, it is possible that testes could play a similar role in energy requirements of males. For winter fish, the level of follicular atresia is much lower. Consequently, winter steelheads produce a larger number of larger eggs than do summer steelheads, which could result in a larger number of larger fry at hatching time. Numbers of fish in summer populations are generally less than those in winter populations, which might be account-

ed for on the basis of fry production. In any event, fecundity of summer steelheads is drastically reduced by reabsorption of eggs immediately prior to spawning while in winter steelheads it is not.

Because of their exposure to temperature extremes in streams during migration it might be expected that summer steelheads would be more tolerant of high temperatures than would winter fish. However, tests with yearlings of the two stocks indicated that resistance time at 25° C for summer fish was significantly shorter than for winter fish. Summer steelhead yearlings were much fatter than winter yearlings, thus lipid quality and tolerance to temperature near the upper lethal level in the two stocks could be associated (Hoar and Cottle, 1952). Nothing is known of the tolerance of adult steelheads to high temperatures.

Detailed examination of meristic series in young steelheads raised under the same conditions indicate small, but persistent differences in some attributes. Very few individuals can be assigned to one population or the other on the

basis of a single character, except for those in a small proportion of each stock which lie at the extremes of range in the character in question. Further, the same characters when used to compare wild adult summer and winter steelheads from different streams in general overlap for all population samples. Nevertheless, these characters which allow statistical separation of experimental populations of F_1 fish provide a reasonable basis for separation of wild, adult summer and winter populations also.

Lindsey (1962) reports examples from the literature where egg size could influence meristic series by providing a larger egg mass, and consequently a larger number of somites during embryonic development. In the present study, correlation between mean egg size and mean vertebral number could not be demonstrated. It should be emphasized that individual female steelhead trout produce eggs of remarkably uniform size, and that variability in size of eggs between females is much greater than that observed in eggs from individual fish. Even slight influence of egg size on vertebral number would therefore likely be

reflected in correlation of mean egg size with mean vertebral count. The fact that no correlation is evident indicates that persistent low vertebral counts in summer steelheads as compared to winter fish represent persistent, genetically influenced meristic differences in the two stocks, both in wild and in experimental F_1 fish.

Mean egg size in summer steelheads tends to be lower than that in winter fish and ranged from a low of 92 mgm for one summer female to a high of 185 mgm for one winter female. From evidence presented by Scott (1962) starvation during final maturation of eggs does not affect egg size in non-anadromous Salmo gairdneri, nor was Scott able to show a significant correlation between egg size and length of female within year-classes or age-classes. In the present study, significant correlation between egg size and size of female could not be demonstrated for six populations of steelhead trout and for one population of non-anadromous S. gairdneri from Kootenay Lake, British Columbia. Notwithstanding lack of correlation between egg size and fish size, there was a strong tendency in population samples for larger fish to produce

larger eggs. Reduction in size of eggs produced by F_1 females of Capilano River origin could be ascribed in part to size of F_1 females at maturity, to lack of exposure to salt water, or to both. There is little doubt that individual females exert strong genetic influence on egg size, but the effects on egg size of female size and environmental conditions during final maturation of eggs are not clear.

Migratory behaviour of steelheads discussed previously indicates that wide differences in sexual development, with concurrent differences in energy stores and levels of performance in surmounting obstacles can result in dispersion of summer and winter steelheads in streams in such a fashion that in many cases little opportunity exists for winter fish to occupy territory readily available to summer stocks. No explanation is offered as to why summer steelheads do not take up residence in the lower portions of rivers commonly utilized by winter fish, and where the spawning gravel may be equal to or superior in quality to that available in upper reaches of streams. In general, headwaters of streams are cooler than lower portions,

and this could be advantageous to a poikilothermic animal under the twin stresses of starvation and sexual maturation while exposed to the vagaries of thermal regimes which fluctuate with climatic conditions. In response to physical conditions, the two stocks can therefore utilize more widely the total stream environment and within these limits, the species can extend its range. Range extensions are of obvious importance to the possibility of adaptation of species to new environmental conditions, and provide the opportunity for selection of characters which may be important in survival of the species.

In Capilano River steelheads, three lines of evidence strongly suggest that reproductive isolation maintains genetically different stocks of summer and winter fish in the same stream. (1) the F_1 progeny of the two stocks can be separated on the basis of visceral fat at age I; (2) vertebral, gill raker and parr-mark numbers are statistically different in F_1 progeny of the two stocks reared under the same environmental conditions; (3) no overlap has been observed in the ratios of gonad weight to body weight when

adult fish mature in salt water. While data are not available for Capilano River as to the separation of stocks by physical barriers, the upper reaches of Capilano River are not as steep as those on Harris Creek, and there would appear to be no impediment to the exchange of genetic material between these stocks except on the basis of behavioural differences. Even where no physical barrier exists, it is likely that the behaviour of adult winter and summer steelheads could effectively provide for the separation of these populations. Summer fish migrate into Capilano River several months earlier than winter fish which would spawn in the same calendar year. Selection of mates and spawning sites, with subsequent defense of territory could preclude the possibility of inter-breeding between summer and winter stocks. Further, summer fish which have been resident in streams for extended periods have well-developed secondary sexual characteristics such as bright red coloration on the lateral line and gill covers, large teeth and hooked jaws. Winter steelheads often enter streams in a near-gravid state, but with little sign externally of

advanced sexual maturation. Such differences in appearance of adult fish could provide a further behavioural barrier to inter-breeding. If summer and winter fish are artificially inter-bred, there is no reduction in viability of such crosses. Thus, progeny of natural crosses could be expected to exhibit physiological and morphological characteristics intermediate between the two stocks. In nature and in experimental groups however, intermediate forms have not been observed, at least with respect to levels of storage fat and development of sexual organs in salt water. Since these two characteristics have been shown to be strongly heritable in Capilano River stocks of summer and winter fish, the evidence is strongly against interbreeding, at least in the Capilano River populations. All other populations of summer and winter steelheads examined to date similarly exhibit characteristics of migratory behaviour and sexual development which clearly place them in one category or the other. In the absence of any evidence to the contrary, the position may therefore be taken that reproductively isolated stocks of these fish occur throughout their range.

It is not known whether residence in fresh water is obligatory for final development of gonads in summer fish. Most specimens of the summer stocks from Capilano River showed no indication that the final maturation phase had commenced in fish reared in a saltwater environment. Summer fish recently arrived from the ocean which were transferred back to salt water showed no external evidence of sexual maturation up to one year later. Thus it would appear that final maturation in summer fish, if not entirely dependent on extended residence in fresh water, is at least rapidly accelerated by freshwater residence and sharply retarded by continued exposure to salt water. Maturation of winter steelheads in nature occurs largely in the marine environment, but marine residence is not obligatory, since all F_1 progeny of Capilano River winter stock matured within three years in the freshwater facilities at Summerland Hatchery.

Fat storage in summer and winter steelhead trout appear to be intimately concerned with patterns of sexual development and migratory behaviour in the two stocks. Summer steelheads have large amounts of storage fat on leaving the

ocean; winter fish do not. Summer steelheads leave the ocean with a gonad/body-weight ratio of approximately 1:100 and not greater than 1:80; winter steelheads generally leave the ocean with a gonad/body-weight ratio of approximately 1:10 and not less than 1:30. Storage levels of visceral fat in young fish are genetically influenced, and yearling summer and winter fish may be separated on the basis of fat storage alone. Fat storage decreases as sexual development proceeds in adult steelheads of both stocks, and lipids constitute a necessary reservoir of materials in summer fish from which energy is available for maintenance of metabolic processes and construction of gonads. The mechanism is not known by which the storage of fat in large quantities is achieved in summer steelheads but not in appreciable amounts in winter steelheads. Since high levels of fat storage occur before summer steelheads migrate to the ocean (Figure 17), it would appear that these fish show evidence of physiological change which pre-adapts them to events in their life history which may not occur before a further two years have elapsed.

Although adult summer steelheads have very large fat reserves on leaving the ocean, the possibility should not be discounted that these fish may also show a further environmental adaptation by reducing metabolic functions to a level below that of winter fish at comparable temperatures. No direct evidence is yet available concerning metabolic rates of summer steelheads in relatively warm water, but in at least two streams (San Juan River and Harris Creek), summer temperatures have been recorded at 18° C, and in 1964 and 1965, summer (daytime) temperatures were consistently above 15° C in Harris Creek and above 17° C in San Juan River, where summer steelheads maintained station for 47 days before moving up a series of cataracts toward their spawning areas. These fish showed no sign of distress or external evidence of debilitation, such as fungus (Saprolegnia) patches commonly associated with the onset of sexual maturity and eventual death of spawning salmonids, nor had their sexual development proceeded past the stage where the ratio of gonad weight to body weight exceeded 1:60. Since these fish maintain a

reserve of energy which enables them to ascend stretches of water not navigable by winter steelheads or Pacific salmon, their resting metabolic rates and energy conservation under exposure to high temperatures could be highly important in setting limits on subsequent performance. Because onset of the final stages of sexual maturation is very slow in summer steelheads, these fish provide a vehicle for the study of physiological processes during maturation which would appear to be unique in Salmo.

Taxonomic characteristics of steelhead trout are variable enough that separation of individuals from the different stocks cannot be made with the use of taxonomic characters alone. Yet even the characters which overlap completely are valuable if they are used with due regard for the possibilities of genetic and environmental effects. From each female steelhead trout artificially spawned, several thousand eggs are available from which to raise progeny. In the present study groups of eggs from single females allowed subsequent statistical comparisons of at least 9 attributes in F_1 fish, and

further comparisons in the F_2 eggs and progeny.

It is apparent that strong parental control operates in both stocks of steelhead trout to regulate size of eggs and numbers of parr-marks, gill rakers and vertebrae. If the progeny from only two sets of parents had been compared, whether between or within stocks, the probability could have been large that the parents differed by such an amount that the progeny might have been statistically separable, yet little biological significance could be ascribed to such an event. From these data it is evident that for the anadromous form of S. gairdneri at least, either a mixture of eggs from several females, fertilized by a mixture of sperm from several males should be used in experimental work, or that progeny from single parental sets should be kept separate. Inheritance of taxonomic characteristics is influenced in such a fashion that progeny from a single set of parents may not be representative of the population of fish from which the parental set was drawn. If progeny from single parental sets are to be compared meaningfully, a large number of parental sets is required.

Several lines of evidence indicate that summer and winter steelheads show consistent differences in their life histories with respect to length of ocean residence, in patterns of sexual maturation and in migration ecology of adult fish. In one stream (Capilano River) F_1 progeny of summer and winter fish were shown to comprise statistically separable stocks when reared under the same environmental conditions. Experimental evidence strongly suggests reproductive isolation for the two stocks in Capilano River and is corroborated by field studies, at least with respect to maturation history and fat storage in populations from a number of widely separated streams. Since viability is not lowered in reciprocal crosses in these stocks, it would appear that reproductive isolation has been achieved comparatively recently. Steelheads, as well as non-anadromous S. gairdneri, are flexible enough in their reproductive habits that well delineated physiological races can develop rapidly in response to strong selective pressure. As a result, two stocks of the same species can extend the range of usable breeding habitat within

the same stream system. Maintenance of reproductively isolated stocks is difficult to assess, but clues are provided by an examination of the interaction of maturation physiology and migratory behaviour (and possibly spawning behaviour) with stream environments. These conditions are summarized in Table XV.

Evolutionary tendencies in stocks of summer and winter steelheads may be assessed in different ways. Some forms of Salmo gairdneri (non-anadromous rainbow trout) may spend their entire lives resident in fresh water lakes or streams, while others (winter steelhead) exhibit patterns of anadromy similar to Pacific salmon. It could be postulated that summer steelheads represent a transitory form, intermediate between purely freshwater rainbow trout and the fully anadromous winter steelhead. Life history patterns in summer steelheads suggest similarity with non-anadromous rainbow trout because the maturation period is spent in freshwater. On the other hand, there is no evidence to suggest that migratory behaviour of young steelheads is not the same or similar in summer and winter stocks. Withler (1966) has shown that the freshwater life of summer and winter steelheads culminates in seaward migration in the first to fourth years, while there

Table XV Events during migration of adult summer and winter steelhead trout from salt to fresh water and during final maturation and spawning in streams.

SUMMER STEELHEAD	WINTER STEELHEAD
TIME OF MIGRATION	
Early May - late August; migration generally maximized in July; variable between streams; relatively predictable for each stream.	Late September - early May; migration generally maximized in February or March; variable as in summer steelhead; relatively predictable for each stream.
PHOTOPERIOD	
Photoperiod long and increasing toward maximum as migration is maximized; decreasing in latter part of migratory period; in some streams migration almost entirely during decreasing photoperiod.	Photoperiod short but increasing during maximum of winter migration; decreasing in early (September through December) portion of migratory period; long and increasing during late (April-May) portion of migration.
STREAM FLOW	
Generally dropping to summer minimum as migration maximized; rising to autumn maximum after fish have taken up stream residence; dropping to winter minimum during final maturation.	Often high but dropping to winter minimum as fish enter streams from ocean; often increasing to spring maximum during latter part of migration and final maturation.
STREAM TEMPERATURE	
Approaching or at summer maximum during maximum migration; at or near autumn maximum as fish "hold" in pools; rising from winter minimum during final maturation and spawning.	At or near winter minimum during maximum migration; rising from winter minimum during final maturation and spawning.
TIME OF SPAWNING	
Not known for most populations; wild fish held in hatchery have matured as early as March 15; wild fish captured in San Juan River gravid as early as February 14; from hatchery records, probably dependent in part on water temperature.	Not known for most populations; spawned-out fish captured by anglers in February; not uncommonly winter steelheads still migrating from ocean early in May in gravid condition; probably dependent in part on water temperature.

appears to be virtually no tendency for seaward migration or anadromous habit in fish derived from freshwater stocks (Neave, 1944). A second hypothesis could be advanced which could categorize summer steelheads as primarily resident freshwater trout which casually invade the marine environment. Lack of substantial populations of resident freshwater S. gairdneri in most coastal streams frequented by steelheads strongly suggests that summer and winter steelheads are similarly anadromous and that resident rainbow trout are not, although exceptions have been recorded (Needham and Gard, 1959). Hoar (1953) points out that territorial behaviour is closely associated with stream residence of salmonids, but comparisons of behaviour between anadromous and non-anadromous S. gairdneri in streams have not yet been made. Thus, the affinities of steelhead trout and freshwater S. gairdneri are not clear, and require further elucidation. It is apparent that with respect to sexual development upon entry to freshwater from the ocean, no intergrades occur between summer and winter stocks. In populations of other Pacific salmonids migrating in spawning streams (e.g. kokanees, five species of anadromous Pacific salmon, Dolly Varden char and others) immature gonads have not been found in fish which remain in

streams and spawn. The summer steelhead thus appears to constitute a variant within the S. gairdneri complex which is unique to the anadromous form of this species.

Differentiation of summer and winter steelhead stocks has not proceeded to the point where they can be assigned to different species, at least not on the basis of widely accepted taxonomic criteria such as comparisons of morphological and meristic characters, the ranges of which overlap in all populations examined to date. The potential is high for further divergence in summer and winter stocks of steelhead trout, because the mechanisms which are operating to preserve reproductive isolation appear to confer an advantage on summer fish for range extension in river systems into habitat which is seldom, if ever, available to winter steelheads. It would appear that physiological differences which result in differences in migratory behaviour of adults have arisen recently, because morphological and meristic differences are still relatively small. These physiological differences likely will continue to result in behavioural differences which will keep these stocks separated until species status is achieved.

LITERATURE CITED

Alm, G., 1949. Influence of heredity and environment on various forms of trout. Institute of Freshwater Research, Drottningholm. Ann. Rpt. No. 29: 29-54.

Bailey, R.M., 1960. A list of common and scientific names of fishes from the United States and Canada. 2nd ed. Amer. Fish. Soc. Special Publ. No. 2.

Berg, L.S., 1934. Vernal and hiemal races among anadromous fishes. Izvestiia Akad. Nauk SSSR, Otd. Mat. i Estestvennyk Nauk for 1934, No. 5, pp. 711-732. (Translation by W. E. Ricker in J. Fish. Res. Bd. Canada, 16 (4): 1959)

Black, E.C., 1952. Upper lethal temperatures of some British Columbia freshwater fishes. J. Fish. Res. Bd. Canada, 10 (4): 196-210.

Carl, G. C., Clemens, W. A. and C. C. Lindsey, 1959. The Freshwater fishes of British Columbia. British Columbia Provincial Museum, Handbook No. 5, 3rd Edition, 192 pp.

Cartwright, J. W., 1959. Egg size and egg number in some freshwater fishes of British Columbia. Unpubl. M. Sc. Thesis, Dept. Zoology, Univ. British Columbia, Vancouver, British Columbia.

Garside, E. T. and F. E. J. Fry, 1959. A possible relationship between yolk size and differentiation in trout embryos. Can. J. Zool., 37:383-386.

Hoar, W. S. and M. K. Cottle, 1952. Dietary fat and temperature tolerance of goldfish. Can. J. Zool., 30:41-48.

Hoar, W. S., 1953. Control and timing of fish migration. Biol. Rev., 28:437-452.

1963. The endocrine regulation of migratory behaviour in anadromous teleosts. Proc. XVI Int. Congress Zool., Washington, D. C., Specialized Symposia, Vol 3:14-20.

Lindsey, C. C., Northcote, T. G. and G. F. Hartman, 1959. Homing of rainbow trout to inlet and outlet spawning streams at Loon Lake, British Columbia. J. Fish. Res. Bd. Canada, 16(5):695-719.

Lindsey, C. C., 1962. Experimental study of meristic variation in a population of threespine sticklebacks, Gasterosteus aculeatus. Can. J. Zool., 40:271-312.

Maher, F. P. and P. A. Larkin, 1955. Life history of the steelhead trout of the Chilliwack River, British Columbia. Trans. Amer. Fish. Soc., 84:27-38.

Neave, F., 1944. Racial characteristics and migratory habits in Salmo gairdneri. J. Fish. Res. Bd. Canada, 6(3):245-251.

1949. Game fish populations of the Cowichan River. J. Fish. Res. Bd. Canada, Bull. No. 84:32 pp.

Needham, P. R. and R. Gard, 1959. Rainbow trout in California and Mexico, with notes on the cutthroat series. Univ. Calif. Publ. in Zoology, 67(1):124 pp.

Northcote, T. G., 1962. Migratory behaviour of juvenile rainbow trout, Salmo gairdneri, in inlet and outlet streams of Loon Lake, British Columbia. J. Fish. Res. Bd. Canada, 19(2):201-270.

Pautzke, C. F. and R. C. Meigs, 1940. Studies on the life history of the Puget Sound steelhead trout, Salmo gairdnerii. Trans. Amer. Fish. Soc. 70:209-220.

Rich, W. H. and H. B. Holmes, 1929. Experiments in marking young chinook salmon on the Columbia River, 1916 to 1927. Bull. U. S. Bur. Fish., 44:215-264.

Richardson, Sir John, 1836. Salmo gairdneri, Gairdner's salmon. In Fauna Boreali-Americana, pp. 221-222. Richard Bentley, London.

Ricker, W. E., 1959. Evidence for environmental and genetic influence on certain characters which distinguish stocks of the Pacific salmons and steelhead trout. Fish. Res. Bd. Canada, Nanaimo, British Columbia, M.S., 129 pp. (mimeo).

Rounsefell, G. A. 1958. Anadromy in North American Salmonidae. U. S. Fish and Wildlife Service, Fish. Bull. 58(130):83-169.

Royal, L. A., 1961. The effects of regulatory selectivity on the production of Fraser River sockeye. Can. Fish. Cult., 14:1-12.

Scott, D. P., 1962. Effect of food quantity on fecundity of rainbow trout, Salmo gairdneri. J. Fish. Res. Bd. Canada, 19(4):715-731.

Shapovalov, L. and A. C. Taft, 1954. The life histories of the steelhead rainbow trout, Salmo gairdnerii gairdnerii, and silver salmon, Oncorhynchus kisutch, with special reference to Wadell Creek, California, and recommendations regarding their management. Calif. Fish and Game, 98:375 pp.

Smith, S. B., 1955. The relation between scale diameter and body length of Kamloops trout, Salmo gairdnerii kamloops. J. Fish. Res. Bd. Canada, 12(5):742-753.

1960. A note on two stocks of steelhead trout, (Salmo gairdnerii) in Capilano River, British Columbia. J. Fish. Res. Bd. Canada, 17(5):739-742.

1961. Selectivity and hybridization in management of fish stocks. Can. Fish Cult., 29:1-6.

Taylor, G. T. and R. J. LeBrasseur, 1957. Distribution, age and food of steelhead trout, Salmo gairdneri caught in the northeast Pacific Ocean, 1956. Fish. Res. Bd. Canada, Prog. Rpt. 110:9-11.

Vernon, E. H., 1957. Morphometric comparison of three races of kokanee (Oncorhynchus nerka) within a large British Columbia lake. J. Fish Res. Bd. Canada, 14(4):573-578.

Withler, I. L., 1966. Variability in life history characteristics of steelhead trout (Salmo gairdnerii) along the Pacific coast of North America. J. Fish. Res. Bd. Canada, 23(3):365-393.

Zarnecki, S., 1963. Wystepowanie populacji sezonowych u lososia atlantyckiego (Salmo salar L.) oraz u troci (Salmo trutta L.) w rzece Wisle — Differentiation of Atlantic salmon (Salmo salar L.) and of sea trout (Salmo trutta L.) from the Wisla (Vistula) river into seasonal populations. Acta Hydrobiol., 5(2-3):255-294. (English summary)

Canada, 14(4):573-578.

Mirhirei, I. M., 1988. Variability in life history characteristics of steelhead trout (Salmo gairdneri) around the Pacific coast of North America. J. Fish. Res. Bd. Canada, 25(3):385-393.

Sarnecki, S., 1961. Wystepowanie bocznicy sezonowych u lososia atlantyckiego (Salmo salar L.) oraz u troci (Salmo trutta L.) w rzece Wiśle — Differentiation of natural salmon (Salmo salar L.) and of sea trout (Salmo trutta L.) from the Wisła (Vistula) river two seasonal populations. Acta Hydrobiol., 2(3-3):255-304. (Polish summary)

Vernon, E. H., 1957. Morphometric comparison of three races of kokanee (Oncorhynchus nerka) within a

B29888